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THE QUARTERLY REVIEW *of* BIOLOGY

THE PHYSIOGNOMY OF INSECTS

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Ante omnia scire convenit naturam corporis, quia alii graciles, alii obesi sunt; alii calidi, alii frigidiores; alii humidi, alii sicciores; alios adstricta, alios resoluta alvus exercet. Raro quisquam non aliquam partem corporis imbecillam habet.—Celsus, Lib. I. Cap. III.

AN ENTOMOLOGIST no less interested in his fellow men than in the insects may with increasing years of observation find increasing resemblance between the two—some insects seeming almost human and some humans behaving very much like insects. This may be due in part to the fact—if indeed it be a fact—that the entomologist may come to resemble the objects with which he is so constantly occupied. If we can trust the statements of some observers, he may even take on some of the physical peculiarities of the group in which he specializes. We have all known entomologists who looked like grasshoppers, cockroaches, bumble-bees or Histerid beetles. The confusion is increased by the fact—and this has not escaped the cartoonists—that there is a certain resemblance between the human and insect body, with its division into head, thorax, and abdomen. And although the insect body has too many appendages and certainly too many wings to suit any human being this side of Paradise, nevertheless the face, head, and eyes of some Orthoptera, Coleoptera, Hymenoptera, and Diptera are very suggestive of certain physiognomies which we daily encounter in the streets and trolley-cars of our great cities. In certain ancient entomological works, purporting to be of a serious character, for example in Jonston's *Theatrum universale omnium animalium* (1718), the heads of insects are often drawn with the obvious intention of accentuating their resemblance to human countenances.

HUMAN TYPES

Those who devote all their attention to our own highly polymorphic species, which Linnæus, I suspect, somewhat sarcastically called *Homo sapiens*, have repeatedly endeavored to group its various individuals in categories according to their temperaments and physical peculiarities. As a result, a number of human types have been distinguished and named

by a long series of investigators, most of whom agree that the pure types are best studied among the young adult males of the species. Two of the types, which have been recently called the "asthenic" and the "pycnic" by Kretschmer (1922), stand out conspicuously and will be recognized at once by the following diagnoses:

The asthenic is pale, scrawny, long-limbed, with narrow head and face ("hatchet-faced"), long, narrow, straight nose, small, often receding chin, narrow chest and abdomen, deficient development of fat and musculature, reduced pilosity on the body but often with abundant cranial thatch, abstemious, dyspeptic, with a tendency to tuberculosis, and when insane, schizophrenic, i.e., prone to fixed ideas, ideas of persecution, etc. This type is active, intense, intellectual, self-centered (introverted), often deficient in a sense of humor, fond of reforming, dogmatic or fanatical, and not infrequently detestable when claiming a too intimate knowledge of the Almighty's plans for making the world safe for democracy. The pycnic—so called, not because he likes picnics, though no other type is so fond of them—but from the Greek word πυκνός, meaning compact or thickset—is rubicund, rotund, large-bodied, short-limbed, broad through the chest, but broader through the abdomen, with round or pentagonal face, pug or thick nose, moderately pilose, fond of eating and drinking, eupeptic, with a tendency to apoplexy and arteriosclerosis; on the mental side cyclothymic, i.e., predisposed to the recurring, circular or manic-depressive forms of insanity, such as melancholia; extroverted, socially easy-going, tolerant in morals and religion and often very lovable because claiming no inside information in regard to the Almighty's designs.

These two types in their purity are sufficiently frequent among our American population. Kretschmer seems to have found the pycnics very common among the Swabians, who are generally characterized by the Germans as "gemütlich" or "gutmütig." The popular distrust of the asthenic and fondness for the pycnic is indicated by the fact that Satan, or Mephistopheles is usually represented as an asthenic while the favorite gods and saints of China and Japan are depicted as fat pycnics. When the belief in Satan was more vigorous than it is at present, he and his demons were often represented as belonging to the athletic type. [See the pictures from the twelfth to the sixteenth century and especially the frontispiece from Didron's *Christian Iconography* in Bonner (1913)]. Why the people should have chosen a symbol like Uncle Sam to represent the United States and one like John Bull to represent England was not altogether clear till the passage of the Volstead Act. Among historical figures the reader will recall Cassius (as depicted by Shakespeare), Dante, Savonarola, Torquemada and John Calvin as asthenics and Falstaff (as conceived by Shakespeare), Martin Luther and ex-President Taft as pycnics. In fiction Don Quixote and Sancho Panza are good examples of the two types. Bud Fisher's creation of Mutt and Jeff may also be cited in this connection.

The great mass of human individuals, however, may be regarded as blends or mosaics of the two types in varying proportions. Even during the lifetime of the same individual, the asthenic may predominate at one time, the pycnic at another. Often the young are asthenic and become pycnic with advancing years, and we have all seen examples of the reverse transformation of pycnic youngsters into asthenic oldsters. Undoubtedly the endocrine glands, and especially the thyroid, pituitary and interstitial glands,

are concerned in the production of both the extreme and the intermediate types.

Among the latter Kretschmer recognizes several categories. One of these is the "athletic," which I need not describe as the reader is familiar with its physical and mental peculiarities from the football and baseball field, the gymnasium, vaudeville stage and movies. Kretschmer further distinguishes "dysplastic" types, which show more or less pathological defect- or excess-development (hypoplastic or hyperplastic development) in certain characters, but I shall pass over these distinctions and for the sake of brevity and clearness call all the intermediates athletic.

The same or similar types have been recognized by other investigators and have been reviewed by Bauer (1924). The asthenic, athletic and pycnic types of Kretschmer evidently correspond to the phthisic, athletic and plethoric habitus of de Giovanni and to Beneke's microsomatic, microplastic, microskelic, longi-

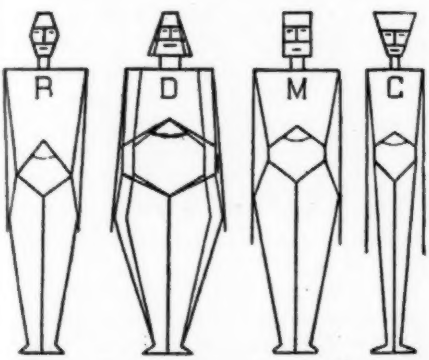

Fig. 1. The Four Human Types of Claude Sigaud, Schematized by Pierre Robin

lineus or longitypus and megalosomatic, euryplastic, brachyskelic, brevilineus or brachytypus, with the intermediate normosplanchnic, normosomatic, mesoplastic, normolineus, normotypus. The two extreme types correspond to Viola's microsplanchnic, or phthisic habitus and megalosplanchnic, or apoplectic habitus, to Bryant's carnivorous and vegetarian

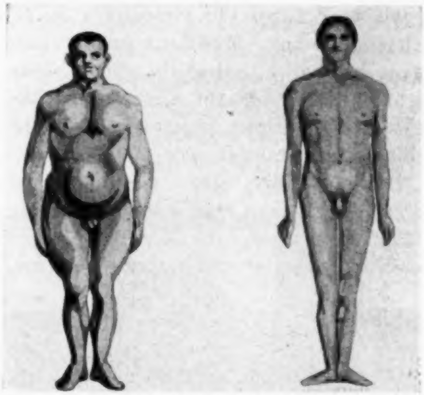

Fig. 2. Idealized "Round" and "Flat" Colloidal Human Types, According to MacAuliffe (Taken from A. Thooris: *La vie par le Stade*)

types, Bean's hypermorph and mesomorph types, Stockard's linear and lateral types, etc. Obviously the pycnic type is that of the human infant. According to Stockard (1923) "the linear type is the faster growing, high metabolizing, thin but not necessarily tall group, while the lateral type is slower in maturing and is stocky and rounder in form."

The French school, following Sigaud and including his pupils Chaillon, MacAuliffe and other contributors to the very interesting *Bulletin de la Société d'Etude des Formes Humaines*, recognize four human types, the respiratory, digestive, muscular and cerebral (fig. 1). The digestive corresponds to the pycnic, the cerebral to the asthenic, the muscular and respiratory to the athletic type of Kretschmer. In a recent paper MacAuliffe (1925) distinguishes a "round" and a "flat" type (fig. 2), which correspond to the pycnic and asthenic respectively, and refers their differences to differences in the col-

loidal state of their tissues, the former consisting of strongly, the latter of feebly hydrophilous gels. The cells of the bibulous pycnic have great osmotic powers, those of the asthenics a feeble surface tension. "The flat type functions more economically than the round. It is also probable that the electric polarization of the cellular surfaces is higher in this latter human category."

Bauer studied the distribution of Sigaud's four categories among 2000 male Viennese and found the following proportions of pure type: respiratory 18 per cent,

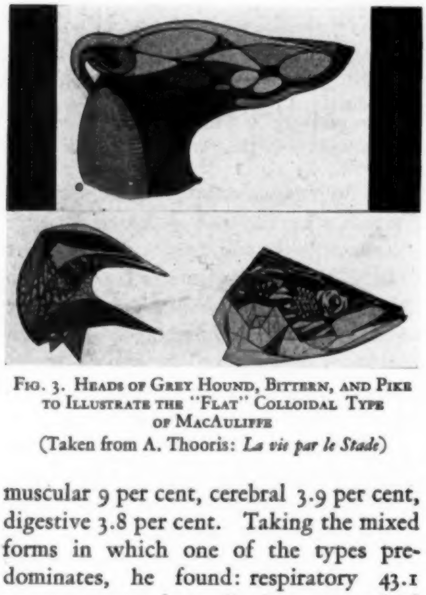

FIG. 3. HEADS OF GREY HOUND, BITTERN, AND PIKE TO ILLUSTRATE THE "FLAT" COLLOIDAL TYPE OF MACAULIFFE
(Taken from A. Thooris: *La vie par le Stade*)

muscular 9 per cent, cerebral 3.9 per cent, digestive 3.8 per cent. Taking the mixed forms in which one of the types predominates, he found: respiratory 43.1 per cent, muscular 23.8 per cent, cerebral 18 per cent, digestive 6.6 per cent. The remaining 8.5 per cent could not be included in any one of the categories. Zweig, one of Bauer's students, studying the same material disproved Sigaud's view that the types do not change with age, although it was clear that each is fixed in youth in its general characters. The digestive type increases with age. Sigaud's schema is not easily applicable to females. Bauer divides them according to the distribution of fat on their bodies into (1) "Reithosentypus" (with fat on hips); (2) fat on arms, breast and neck, but with thin legs; (3) fat on thighs and legs, but poorly developed on trunk; (4) fat on breasts and gluteal region (steatopygous type).

ANALOGUES OF HUMAN TYPES AMONG ANIMALS

Now it is interesting to note that all the main types exhibited by the single species *Homo sapiens* have their analogues in most groups of animals and even among the plants. As examples of the asthenics and pycnics I mention only the following: among our domestic animals the greyhound and King Charles spaniel (figs. 3 and 4) and among other mammals the giraffe and armadillo, among the birds the herons and finches (figs. 3 and 4), among reptiles the tree-snakes and box-tortoises, among the amphibians the coecilians and toads, among fishes the eels and box-fishes; among crustaceans such forms as *Caprella* and the crabs; among Echinoderms the brittle-stars and the sea-urchins; among myriopods *Geophilus* and *Glomeris* and among plants the vines and the melon-cacti. Between the extremes in each case we find the great majority of species, the athletes, which exhibit a more nearly average development of their organs.

Of course, the insects, which are represented on our planet by such a bewildering number and variety of highly specialized species, may be expected to show the asthenic and pycnic types in a very pronounced form. There are, in fact, in all the principal orders, whole genera or even families of the two types. For purposes of illustration I have brought together a series of these insect Mutts and Jeffs in the accompanying figures (figs. 5 and 6).

As the reader is familiar with them or with similar forms I shall not stop to designate the various tenuous walking-sticks, grasshoppers, ants, dragon-flies, crane-flies, mosquitoes, ant-lions, panorpids, etc., nor the many chunky bugs, beetles, moths, etc. The reader will notice that the latter insects, like some human pycnics, have large rotund bodies and rather short, slender legs, and will recall certain ently and often unsuccessfully wrestling with them, will certainly not object.

The general impression produced by the insect asthenics and pycnics is that of mutations which have somehow managed to survive among the great mass of athletic species, but it is doubtful whether they have arisen as such saltatory variations. The asthenics are more archaic or at least more frequent in ancient and

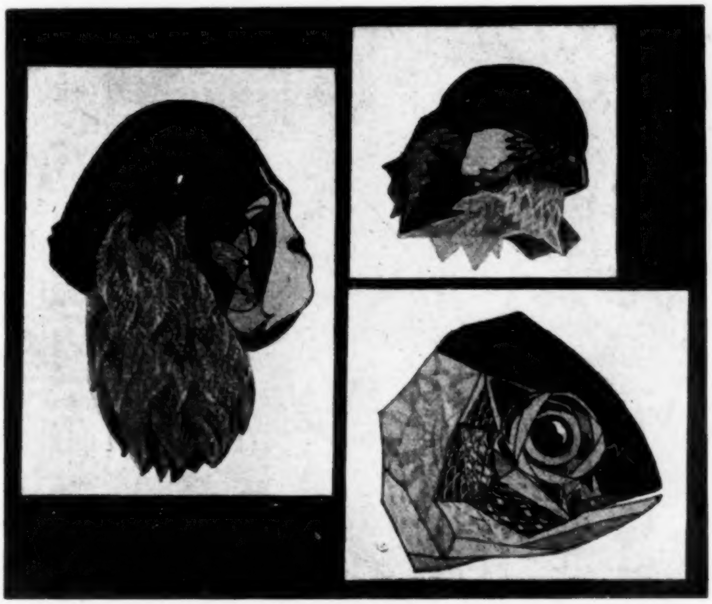

Fig. 4. Heads of King Charles Spaniel, Finch, and Bream, to Illustrate the "Round" Colloidal Type of MacAuliffe
(Taken from A. Thooris: *La vie par le Stade*)

cases of both types occurring in succession in the same species, as, e.g., in the ant-lion, which has a pycnic larva and an asthenic adult, and the flea which has an asthenic larva and a rather pycnic adult. Among the insects, too, the great majority of species are intermediate, and if I designate this group as "athletic" the economic entomologists, who spend their lives ard- primitive orders or suborders, and, with the exception of the mosquitoes and Chironomids, seem often to belong to rather rare, recessive or evanescent species. The differences between the two types cannot be due to the quality of the food, because there are predatory and phytophagous species in both groups. That they differ in metabolism is probable.

The pycnics, like their human analogues, are certainly great feeders compared with the asthenics—compare, e.g., the appetite of a dung-beetle with that of a walking-stick insect. And structurally there is a great difference in musculature, the muscles of the asthenics being long and slender while those of the pycnics are short and voluminous. This matter of the musculature in these and other insects—a matter as much neglected by recent insect morphologists as it was emphasized by those of former times—I should like to place in the center of the following discussion, because, as we shall see, it is the musculature that mainly determines the physiognomy of insects.

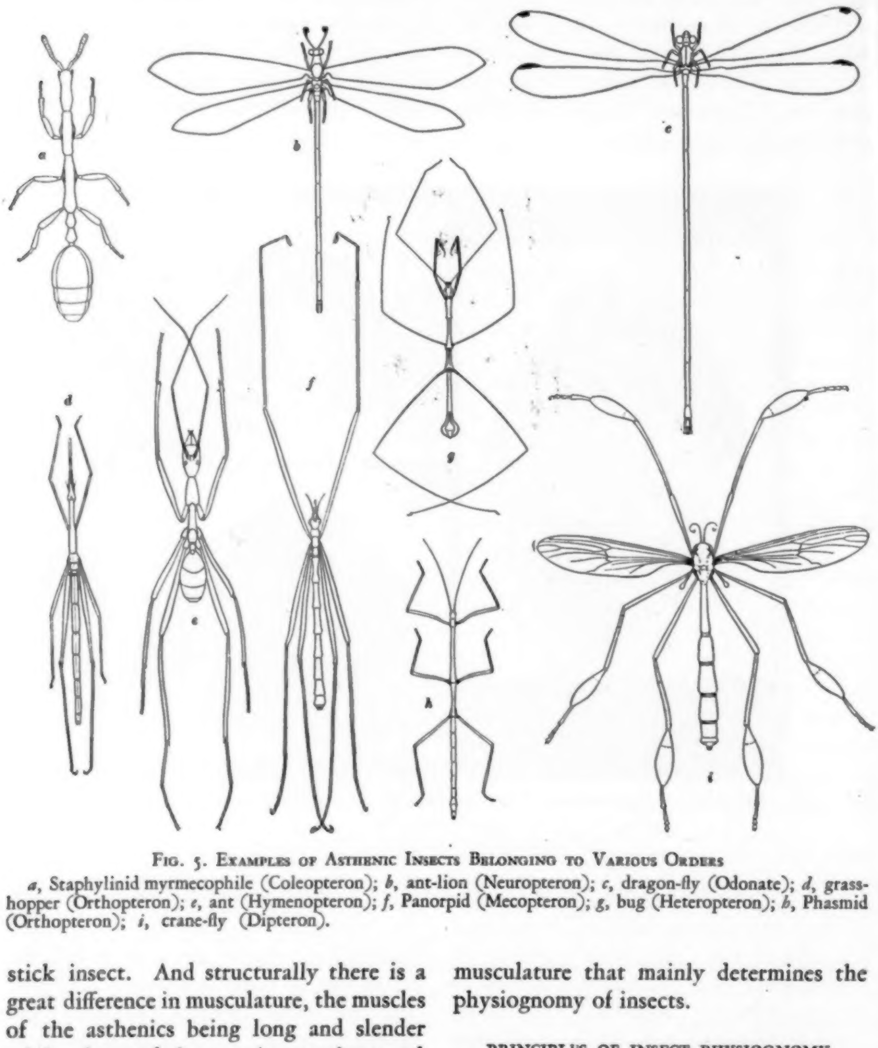

FIG. 5. EXAMPLES OF ASTHENIC INSECTS BELONGING TO VARIOUS ORDERS

a, Staphylinid myrmecophile (Coleopteron); *b*, ant-lion (Neuropteron); *c*, dragon-fly (Odonate); *d*, grasshopper (Orthopteron); *e*, ant (Hymenopteron); *f*, Panorpid (Mecopteron); *g*, bug (Heteropteron); *h*, Phasmid (Orthopteron); *i*, crane-fly (Dipteron).

PRINCIPLES OF INSECT PHYSIOGNOMY

The reader is familiar with the fact that in insects, as in other arthropods, the musculature is inside the skeleton to

which it is attached and that the shape and size of the various elements of the skeleton depend on the volume and arrangement of the muscles. Here the skeleton and integument are one, whereas in vertebrates the muscles which move the skeletal elements are external to them and immediately beneath the very flexible integument. Hence in vertebrates that are not too scaly, feathery or hairy the play of the musculature is visible from the outside, whereas in insects we are presented with a rigid envelope capable of movement only at well-defined, preformed articulations. Hence, also, the very limited and mechanical expression of the emotions in insects as compared with the wonderful range and subtlety of expression in the human face and body, a range and subtlety so extraordinary that from

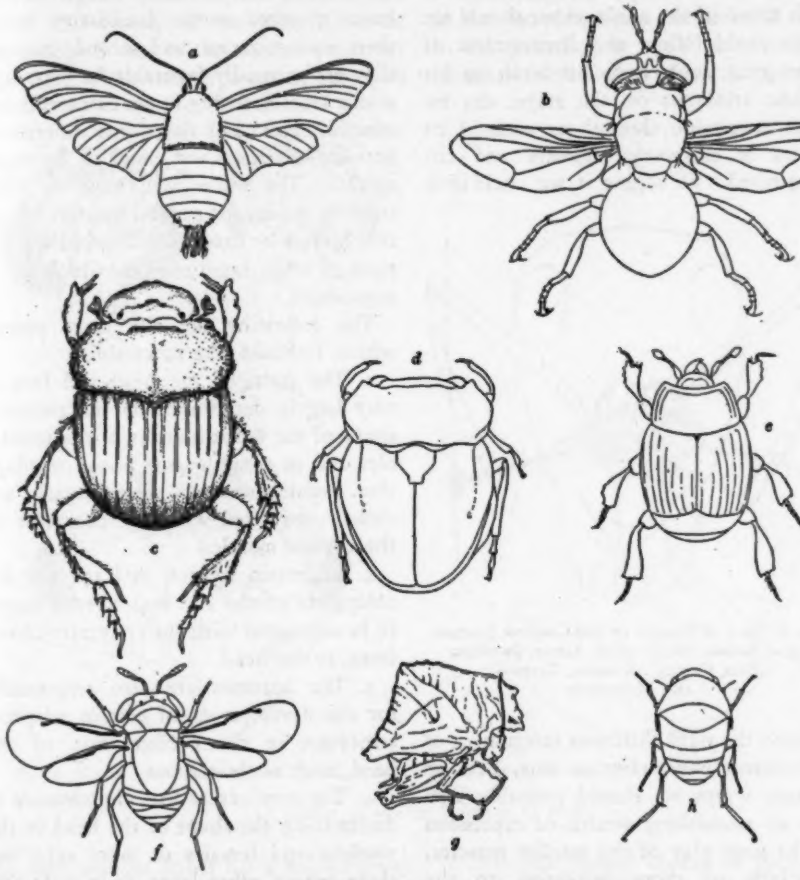

Fig. 6. Examples of Pycnic Insects Belonging to Various Orders

a, Sphingid moth (Lepidopteron); *b*, Syrphid fly (Dipteron); *c*, Lamellicorn beetle (Coleopteron); *d*, bug (Heteropteron); *e*, Histerid beetle (Coleopteron); *f*, Chalcidid fly (Hymenopteron); *g*, grasshopper (Orthopteron); *h*, Phorid fly (Dipteron).

our earliest years it constitutes a means of intercommunication among us second only and very often superior to articulate speech. Moreover, although the powers of facial and bodily expression of the human infant are very limited compared with those of the adult, as we should see if we could follow the development of some great actor from his birth to his highest triumphs on the stage, the insect's expression throughout each of its instars is extremely uniform and circumscribed. Of course if we could look

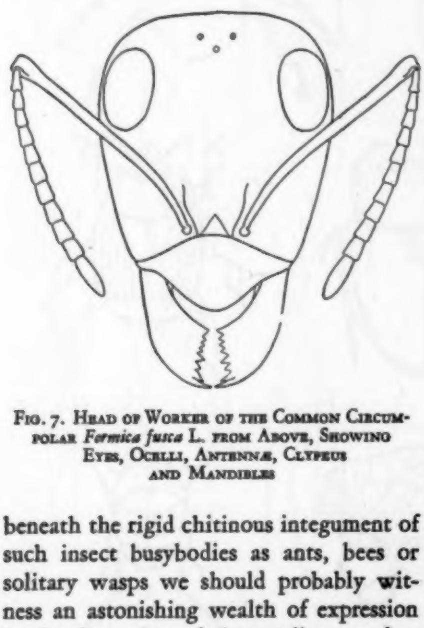

FIG. 7. HEAD OF WORKER OF THE COMMON CIRCUMPOLAR *Formica fusca* L. FROM ABOVE, SHOWING EYES, OCELLI, ANTENNÆ, CLYPEUS AND MANDIBLES

beneath the rigid chitinous integument of such insect busybodies as ants, bees or solitary wasps we should probably witness an astonishing wealth of expression in the finer play of the smaller muscles, especially of those belonging to the viscera.

To trace the correlations between the development of the various muscles and that of the skeletal elements throughout the insect body would prove to be an undertaking as formidable as it would be wearisome. I shall therefore discuss at length only the most interesting region, the head, and confine myself still further very largely to a consideration of the ants. This will be best for two reasons: first, because I have been peering for nearly thirty years into the countenances of so many thousands of these insects that I have acquired some familiarity with their idiosyncracies, and second, because they are unusually favorable for physiognomic studies, owing to the extraordinary morphological and functional differences between the sexes and castes of the same species. The reader will have no difficulty in testing the general validity of my conclusions by extending them to the insects of other families with which he is acquainted.

The following are the main points which I should like to establish:

1. The form of the head and face is very largely determined by the size and shape of the flexor muscles of the mandibles and in turn the functional or adaptive peculiarities of these organs are closely correlated with the character of their flexor muscles.

2. In certain species, at least, the development of the antennal muscles seems to be correlated with the convexity of the front, or forehead.

3. The antennæ are also responsible for the development of certain adaptive structures in the configuration of the head, such as the scrobes.

4. The eyes are of little importance in determining the shape of the head in the workers and females of most ants, but these organs, when large, as in male ants and especially in certain other insects with haustellate mouthparts (Diptera, Lepidoptera, Mecoptera, Heteroptera, etc.) have considerable physiognomic value.

5. Certain head-forms are very largely determined by direct adaptation to the cylindrical cavities in the hard plant tissues or soil inhabited by the insects.

Let us begin with the head of our common *Formica fusca*, an ant of the true Nordic type, the *beau ideal* of the family, with chaste, well-balanced features and beautifully rounded forehead (fig. 7). To a slightly stretched imagination this head will not appear so very inhuman, especially if we let the clypeus represent the nose. The mouth is rather large, to and inserted in the corners of our mouth, we should be equipped very much like an ant. And, no doubt, we should find the whole arrangement delightfully convenient. We could do very rough work with our inferior, or oral pair of hands without in the least impairing our sense of touch in the superior, or nasal pair, and the intimate combination of touch and smell

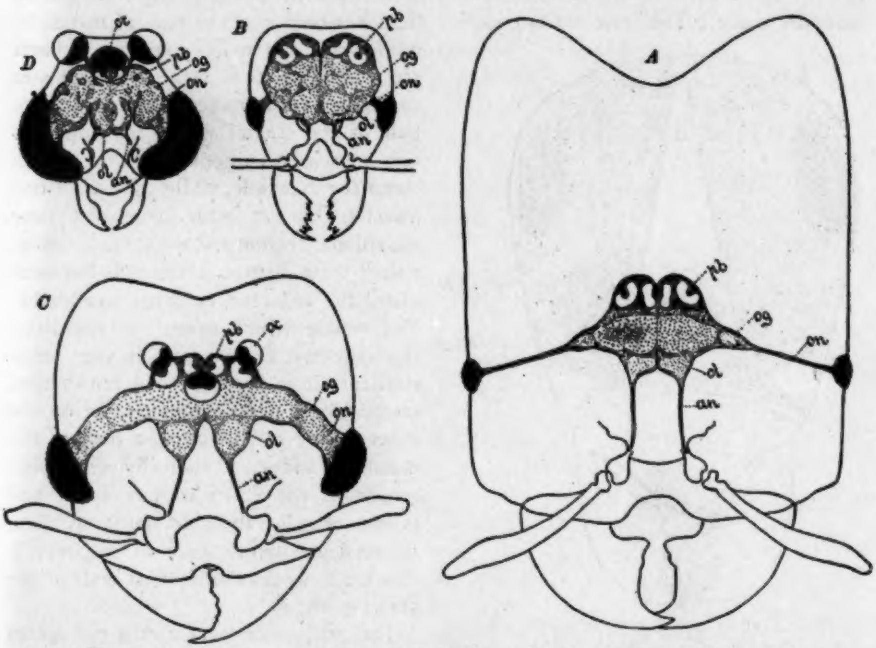

FIG. 8. HEADS AND BRAINS OF THE FOUR CASTES OF *Pheidole instabilis* EMERY FROM TEXAS, DRAWN TO THE SAME SCALE

A, soldier; *B*, worker; *C*, female; *D*, male

be sure, and its upper lip is hidden away under the clypeus. The antennæ and mandibles, however, are decidedly inhuman. But if we imagine our hands and arms split into two pairs of appendages, and one pair thin, mobile, covered with exquisite, intermingled tactile and olfactory organs and inserted just above the base of our nose, and the other, shortened till only the rigid hands remain in this pair would enable us to gain a very satisfactory knowledge of our immediate environment. We should move through the world like ants, continually topochemorecepting the various objects in our path, and we should probably speak of strawberries as soft, rounded-conical odors, of cigarettes as harder, cylindrical odors, table-tops as very hard, smooth, oblong odors of a certain quality, etc.

Judging by superficial appearances we might be tempted to extend the old phrenology of Gall and Spurzheim to the ant and regard the size and shape of its hard cranium as indications of the size and shape of its brain, but when we open its head we see at once that the brain is separated by a considerable space from the cranial wall and that the greater part of the cranial cavity is filled with muscular tissue. The brain varies greatly

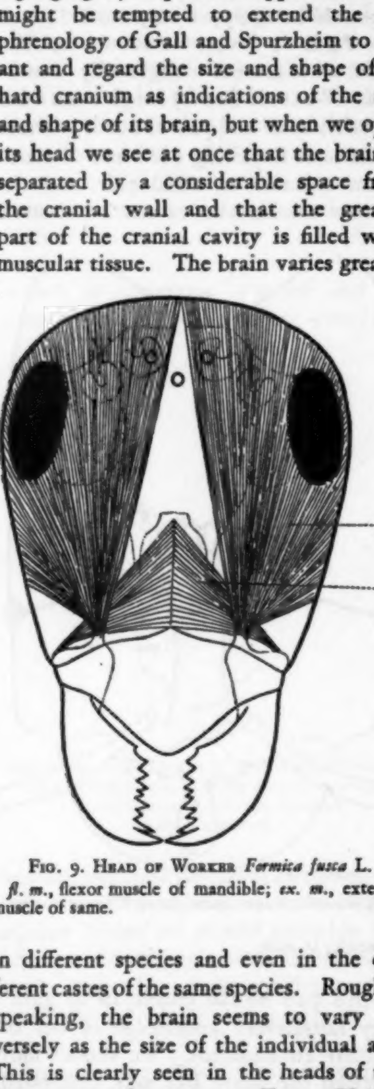

FIG. 9. HEAD OF WORKER *Formica fusca* L.
fl. m., flexor muscle of mandible; *ex. m.*, extensor muscle of same.

in different species and even in the different castes of the same species. Roughly speaking, the brain seems to vary inversely as the size of the individual ant. This is clearly seen in the heads of the four castes of a common Texan *Pheidole* (*Ph. instabilis*) (fig. 8). When the eyes are small or of moderate size, therefore, the head is an index to the muscular powers and not to the intelligence or sensory development of the insect.

CORRELATION OF HEAD SHAPE AND MUSCULATURE OF MANDIBLES

Returning to the head of *Formica fusca* (fig. 9) which has an unusually large brain, and removing the dorsal wall, we observe that on each side of the median line its contents consist very largely of a huge pyramidal muscle, which is attached proximally by a short, stout tendon to the inner corner of the base of mandible, while the gradually expanding fibres are attached distally to a very large area comprising much more than the posterior half of the cranial wall. In some ants this muscle, the contraction of which closes the mandible, really consists of two muscles, but as both have the same mandibular tendon and the same function, I shall treat them as a unit. It has been called the adductor, or flexor mandibulæ. The muscle which opens the mandible, the abductor, or extensor, is very much smaller. It is flattened and fan-shaped, inserted by a short, stout tendon on the outer corner of the extreme base of the mandible and runs ventrally under the tendon of the flexor to spread out and become attached to a thin, chitinous plate, or apodeme, which rises in the middle line from the floor or ventral wall of the cranium, the gula.

The great differences in the volume of the mandibular flexors and extensors is, of course, correlated with differences in their functions. The extensors have merely to open the mandibles, but the flexors have to perform the much more arduous task of seizing, holding, biting, gnawing or crushing the prey or the wood or soil in which the ants' nests are made. We may, therefore, concentrate our attention on this pair of more important muscles, whose development in the various species and castes intimately depends on the structure of the mandibles, and since the mandibles

differ greatly according to the habits of the ants it will be advisable to consider these appendages somewhat more closely. The typical mandible has a three-cornered blade, with a straight or more or less convex, entire outer border and two straight inner borders, one basal and toothless, the other apical and armed with teeth. A great many different types of mandibles may be recognized among the Formicidæ, but I will reduce them to nine: first, ***biting*** mandibles, of moderate size, with subequal internal borders and a moderate number of sharp teeth on the apical border (figs. 7, 9, 12); second, ***gnawing*** mandibles, which are short and stout, with a few broad, strong teeth (fig. 12*a*); third, ***crushing*** mandibles, which are thick and stout, very convex externally, with few or no teeth (fig. 8a, 9a–d); fourth, ***cutting*** or scissor-like mandibles which are broad, flat and rather thin, with sharp, toothed apical border (fig. 11); fifth, ***grappling*** mandibles, which are very long, slender, with long apical border, armed with a few or numerous often unequal teeth (fig. 13–15); sixth, ***clipping*** mandibles, which are long, linear, straight or slightly curved, with a few sharp, abruptly incurved teeth at the apex, and the inner borders toothless, or finely serrate (figs. 16 and 17); seventh, ***piercing*** mandibles, which are slender, sickle-shaped and pointed, without teeth or with minute vestiges of them along the inner border (fig. 18*e–h*); eighth, ***vestigial*** mandibles which are reduced and apparently useless organs, occurring only in the male sex (figs. 10g and 17*b*); ninth, ***aberrant*** mandibles, including a number of singular forms of still unknown function (figs. 19 and 20). Of these various types, the biting, gnawing, crushing and cutting mandibles are large and powerful; the grappling, piercing, clipping, vestigial and aberrant though sometimes of large size are rather weak and therefore furnished with less powerful flexor muscles.

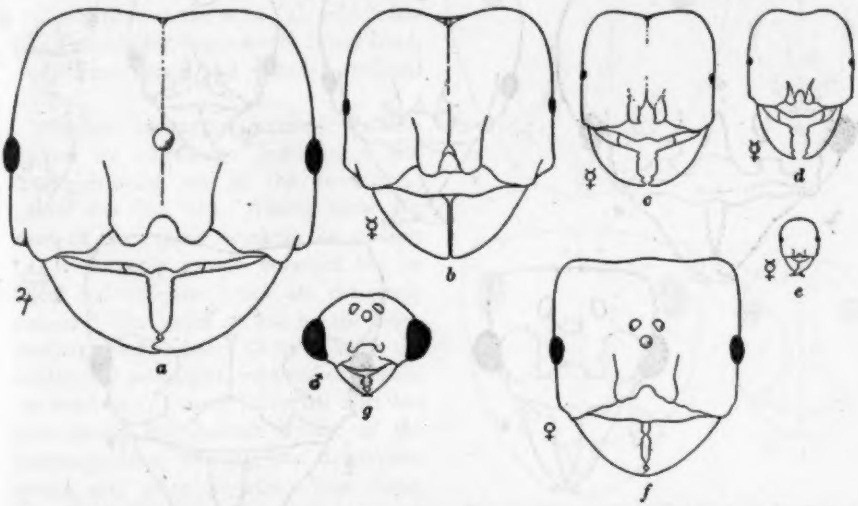

FIG. 10. HEADS OF VARIOUS CASTES OF AN EAST INDIAN HARVESTING ANT, *Pheidologeton diversus* JERDON *a*, soldier; *b* to *d*, intermediate forms between the soldier and worker minima, *e*; *f*, female; *g*, male. Note rounding of occiput correlated with feeble mandibular development in the male and minima.

We may now examine several examples which show very clearly the correlation between the size and development of the mandibles, their flexor musculature and the shape of the head, a correlation so intimate that an expert mathematician might be able to express it in definite formulæ. In figure 21 I have represented the various castes of the harvester, *Pheidole instabilis*. The large individual below (*g*) is the deälated fertile female, or queen, the small winged individual (*h*) is the male; the very large-headed individual (*a*) is the largest type of worker, or soldier, the very small individual (*f*) the worker proper. Between these two extremes we find in any flourishing colony of the species, a complete graded series of intermediates, some of which (*b* to *e*) are represented. The worker (*f*) forages and collects the seeds and stores them in the nest. The big-headed forms may be called the official nut-crackers of the colony because they crush the seeds with their mandibles. You will notice that the head decreases in size and length and in the convexity of its occipital lobes, as indicated by the gradual rounding of the posterior corners and decreasing concavity of the occipital border, till we reach the worker, which has a very small, rounded rectangular head, as broad as long. The crushing mandibles gradually become mandibles of the biting type as we pass from the soldier to the worker proper, and in my preparations the flexor muscles, which in all the forms fill out nearly the whole cranium, show a corresponding gradual decrease in volume.

The same phenomenon is exhibited in

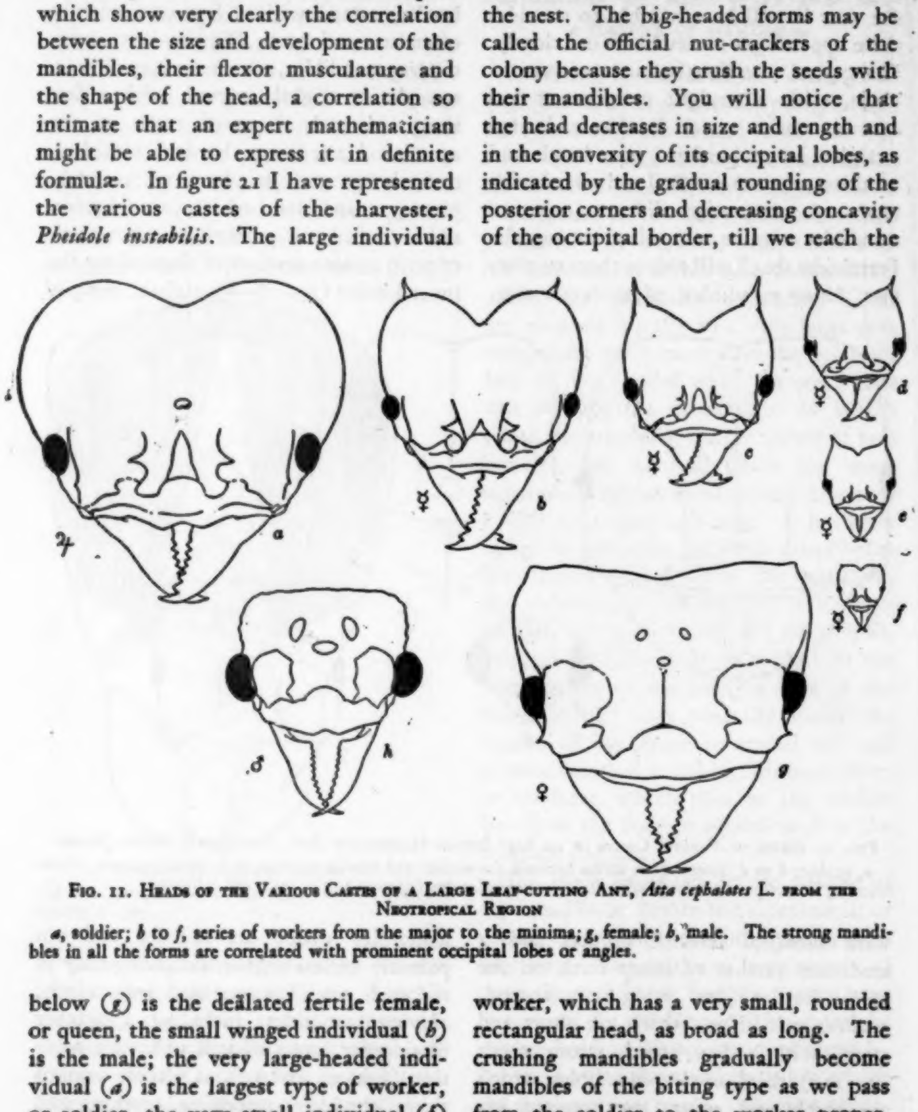

FIG. 11. HEADS OF THE VARIOUS CASTES OF A LARGE LEAF-CUTTING ANT, *Atta cephalotes* L. FROM THE NEOTROPICAL REGION

a, soldier; *b* to *f*, series of workers from the major to the minima; *g*, female; *h*, male. The strong mandibles in all the forms are correlated with prominent occipital lobes or angles.

the Indomalayan harvester, *Pheidologeton diversus* (fig. 10), but in an even more exaggerated form. In this figure only the outlines of the heads of a series of soldier and worker individuals and of the queen and male are represented. In the soldier provision is made for the huge flexor muscles by such a great increase in the width as well as in the length of the head, that the difference between the two extremes of the worker series becomes enormous. The queen's head (*f*) resembles that of the soldier (*a*) but you will notice that the male (*g*), which has small mandibles, has a small, broad head, with very short and rounded occipital region.

Another instructive example is furnished by the large leaf-cutting and fungus-growing ants of the neotropical genus *Atta* (fig. 11). Among these the head of the biggest workers, or soldiers (*a*) is not only greatly enlarged but its front and occipital lobes are extremely convex. The leaves are cut by the intermediate worker castes (*b* to *e*) with the scissor-like mandibles, whereas the smallest workers (*f*) never leave the nest but live among the delicate hyphæ of the fungus-gardens, weeding out deleterious spores and alien mycelia. This caste, which therefore works only on soft materials, has small, weak mandibles and the head is accordingly very much smaller, narrower and less convex. The queen (*g*), which has to dig her nest in the soil and defend her young brood, has a head much like that of the larger workers. The male (*h*), unlike most male ants, has well-developed mandibles and therefore exhibits a much greater development of the head behind the eyes.

The series of worker ants which I have used for illustration recalls the graded series of Harvard professors who have been classified by some of the students as high high-brows, high-brows, low high-brows, high low-brows, low-brows and low low-brows. Some authors regard the soldiers, the highest high-brows of our ant series, as monstrous, or pathological forms on account of the excessive development of their crania. Certain facts might seem to lend support to such an

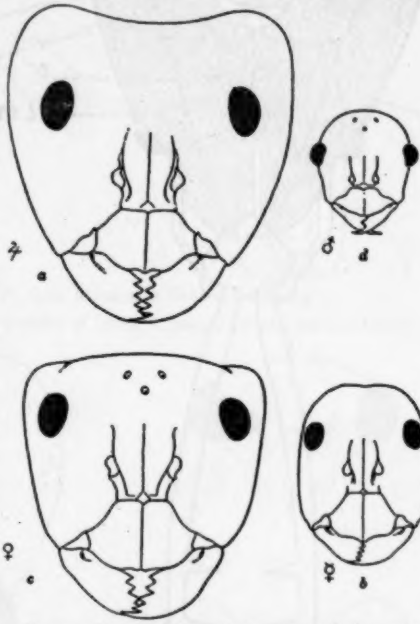

FIG. 12. HEADS OF FOUR CASTES OF AN AUSTRALIAN FORMICINE ANT, *Camponotus* (*Myrmosaulus*) *bellicosus* FOREL

a, worker maxima; *b*, worker minima; *c*, female; *d*, male. Note prominence of occipital corners in *a* and *c* with large mandibles and rounding of occiput in *b* and *d* with feeble mandibles.

opinion. If the soldier of *Ph. instabilis* be placed on its head on a perfectly smooth, hard, horizontal surface, the insect may be quite unable to right itself and may even die standing on its head. But this is a typical laboratory experiment. In its natural environment the soldier never encounters such surfaces. Closer study shows that all these sup-

posedly monstrous forms are really exquisitely specialized and adapted for the functions they have to perform in the life of their respective colonies. The soldiers of the harvesting *Pheidoles* and

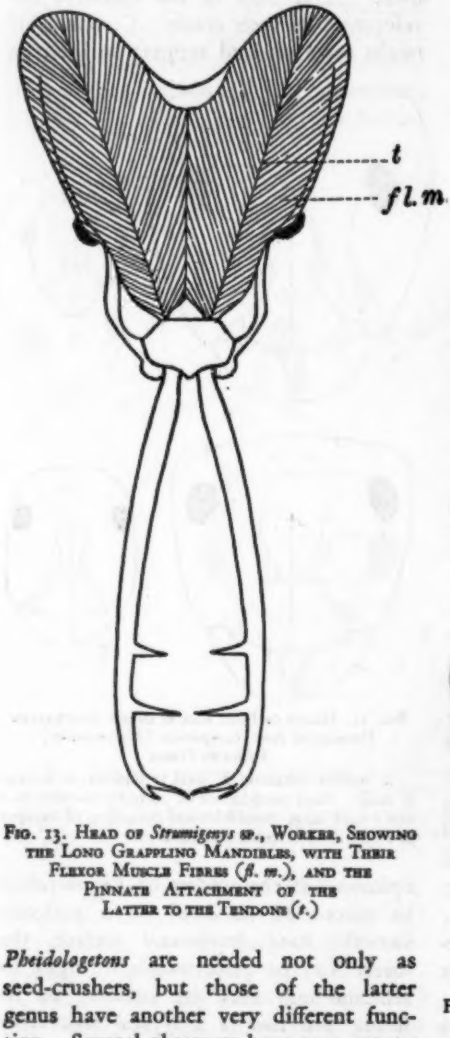

Fig. 13. Head of *Strumigenys* sp., Worker, Showing the Long Grappling Mandibles, with Their Flexor Muscle Fibres (*fl. m.*), and the Pinnate Attachment of the Latter to the Tendons (*t.*)

Pheidologetons are needed not only as seed-crushers, but those of the latter genus have another very different function. Several observers have seen groups of the minute *Pheidologeton* workers sitting quietly on the huge heads of the soldiers and riding to and from the nest. The soldiers of the insect-eating *Pheidoles* dismember the tough prey before or after

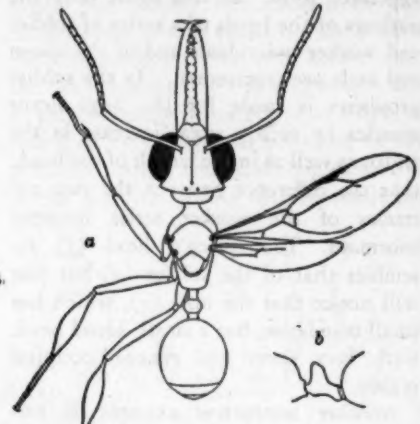

Fig. 14. *Myrmoteras donisthorpei* Wheeler, a Formicine Ant from Borneo
a, female; *b*, petiole. Note the grappling mandibles and huge eyes

Fig. 15. Head of *Acanthognathus lentus* Mann from Central America
(After Mann)

it has been carried into the nest. Hingston (1922, p. 61 et seq.) has recently

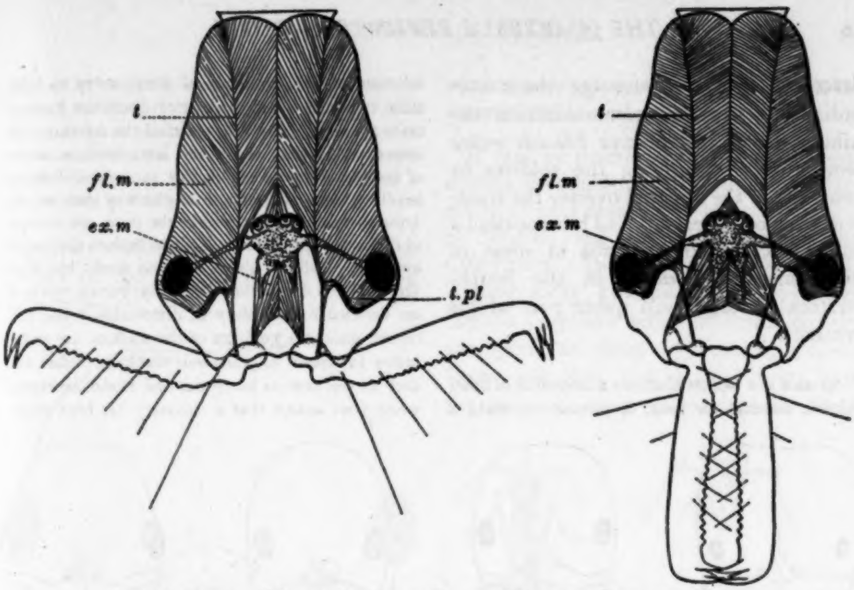

FIG. 16. HEAD OF *Odontomachus vastatus* F. WITH MANDIBLES OPEN AND CLOSED

ex. m., extensor muscles of mandibles; *fl. m.*, flexor muscles of latter; *t.*, tendon; *t. pl.*, plate of tendon

FIG. 17. HEADS OF SOUTH AMERICAN ANT, *Daceton armigerum* PERTY, WITH CLIPPING MANDIBLES

a, head of female; *b*, of male; *c*, of worker. Note the absence of occipital development correlated with vestigial mandibles in the male.

described in vivid language the extraordinary powers of communication exhibited by the diminutive *Pheidole indica* worker when notifying the soldiers to come out of the nest and oversee the transportation of the prey. As I have noticed a somewhat similar behavior in some of our American *Pheidoles* in the Southwestern States, I will quote part of his remarks:

As soon as a worker discovers a caterpillar or other suitable material for food, it proceeds to make a careful examination of its prey. It runs all over the caterpillar exploring it with its sensitive antennæ, shaking it with its jaws and attempting to drag it to the nest. The worker, satisfying itself that the discovery is suitable for storage and finding the removal of it beyond its own weak efforts, hastens off to the nest in great excitement and by the shortest route. It meets another worker on its path; their antennæ meet; the second worker is imbued with the enthusiasm of the first, has received information of the discovery and hastens off to the insect. A third, a fourth, and possibly more workers are similarly informed on the route and all hurry away to lend their assistance. But the excited discoverer hastens on to the nest. Now it has reached the entrance. It enters and is lost to view. In a few seconds a swarm of rushing, bustling and excited ants, come dashing headlong from the nest. From the way they are all lying in readiness just within the door and emerge at the same moment in one body as though they were awaiting a call for aid, I have no doubt but that these ants so divide their labor that certain workers are detailed for the duty of discovering food, and others, under the guidance of the soldiers, are under orders to remain in permanent readiness within the door of the nest to hurry out and render assistance when news arrives that a discovery has been made.

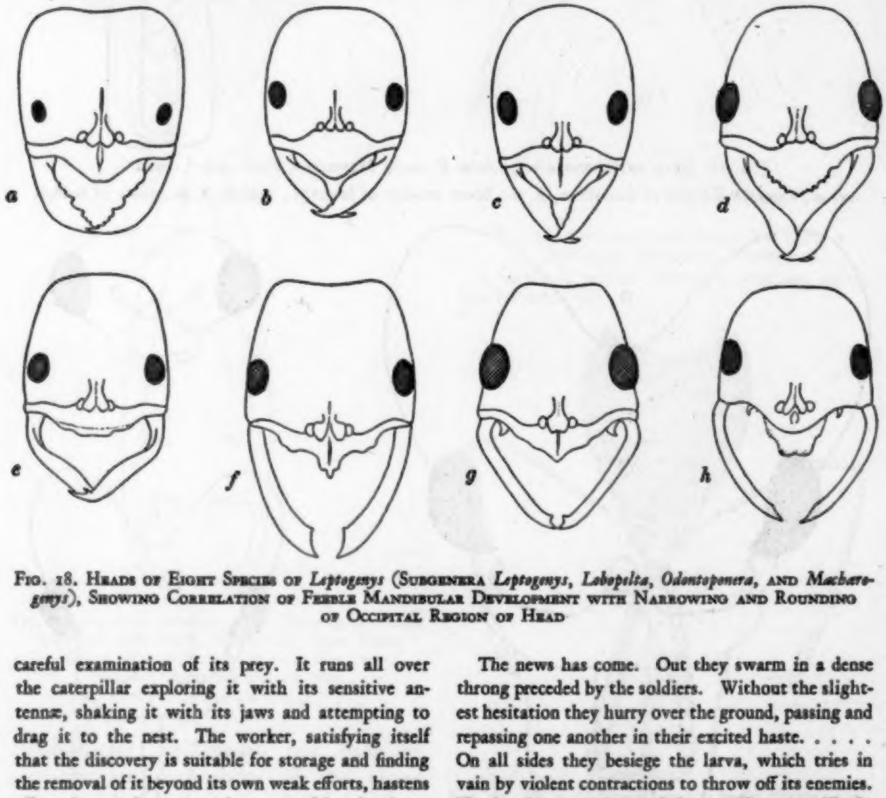

FIG. 18. HEADS OF EIGHT SPECIES OF *Leptogenys* (SUBGENERA *Leptogenys*, *Lobopelta*, *Odontoponera*, AND *Machaerogenys*), SHOWING CORRELATION OF FEEBLE MANDIBULAR DEVELOPMENT WITH NARROWING AND ROUNDING OF OCCIPITAL REGION OF HEAD

The news has come. Out they swarm in a dense throng preceded by the soldiers. Without the slightest hesitation they hurry over the ground, passing and repassing one another in their excited haste. . . . . On all sides they besiege the larva, which tries in vain by violent contractions to throw off its enemies. The battle grows hot and fierce. The caterpillar in its struggles now gains the mastery, but ants hurrying on in increasing numbers gradually overpower it. Workers, at intervals, retire from the battle and hasten back to the nest at the greatest speed to call out more reinforcements and hurl them into the

fight. The caterpillar weakens; it cannot face these repeated additions to the strength of its foes. It is overwhelmed by the force of numbers, soon becomes exhausted, and then lies at the mercy of the ants which, clinging in a body round their powerless victim, drag it slowly to the nest.

Hingston also describes the peculiar behavior of the soldiers during migration to a new nest.

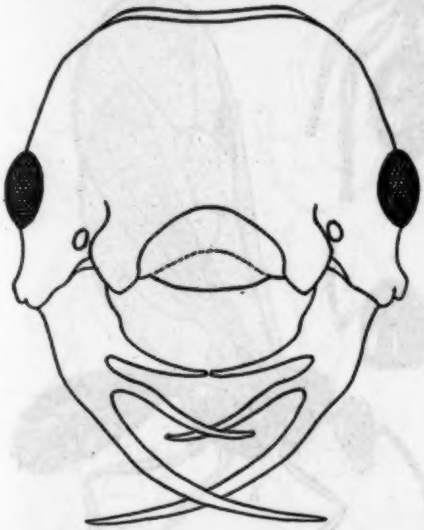

FIG. 19. HEAD OF WORKER OF THE NEOTROPICAL *Thaumatomyrmex ferox* MANN, WITH WEAK, ABERRANT, THREE-TOOTHED MANDIBLES AND UNDERDEVELOPED OCCIPITAL REGION

The main burden of toil falls on the smaller workers. It is they alone that transport the larvæ, and they often carry their companions from nest to nest. The soldiers carry nothing. They are not humble toilers, but are the directors of the transport. They are the aristocracy of ant life. They hurry out of the nest singly and at intervals with a throng of laden ants following in their rear, and as each powerful soldier hastens along the migrating line it looks like an officer leading and directing his company of men. Nor do the soldiers return again to the old nest. The smaller workers, once they have deposited their larvæ in the new nest, hasten back for a fresh burden, but a returning soldier is never seen. It, no doubt, busies itself with important duties within the new nest, but takes no further part in the migrating line.

It may be readily shown that the conditions sketched for the cranial physiognomy of ants obtain also in other groups of insects, and especially among the Coleoptera. Two examples must suffice. Among many Lucanidæ, or stag-beetles (fig. 22) we find series of forms closely analogous to those of *Pheidole*, *Pheidologeton* and *Atta*, but in the beetles it is the males that are polymorphic. They

FIG. 20. A JUMPING PONERINE ANT, *Harpegnathos venator* VAR. *rugosus* WITH ABERRANT MANDIBLES, FROM HONGKONG

a, deälated female, dorsal view; *b*, same, lateral view; *c*, head, from above. (After G. May.)

have been arranged according to the development of the mandibles in series beginning with large macrodont forms, passing through amphiodont, eopriodont and priodont forms and ending with individuals with small mandibles like the female (Griffini, 1905, Champy, 1924). In such a series the head gradually decreases in width *pari passu* with a reduction in the size of the mandibles. There is also a corresponding reduction in the volume of the prothorax and fore legs. This occurs also in the ant series and might be expected, because the muscles that raise, lower and rotate the head are situated in the prothorax. In the highest highbrows among the Lucanids we even find the posterior corners of the head pro-

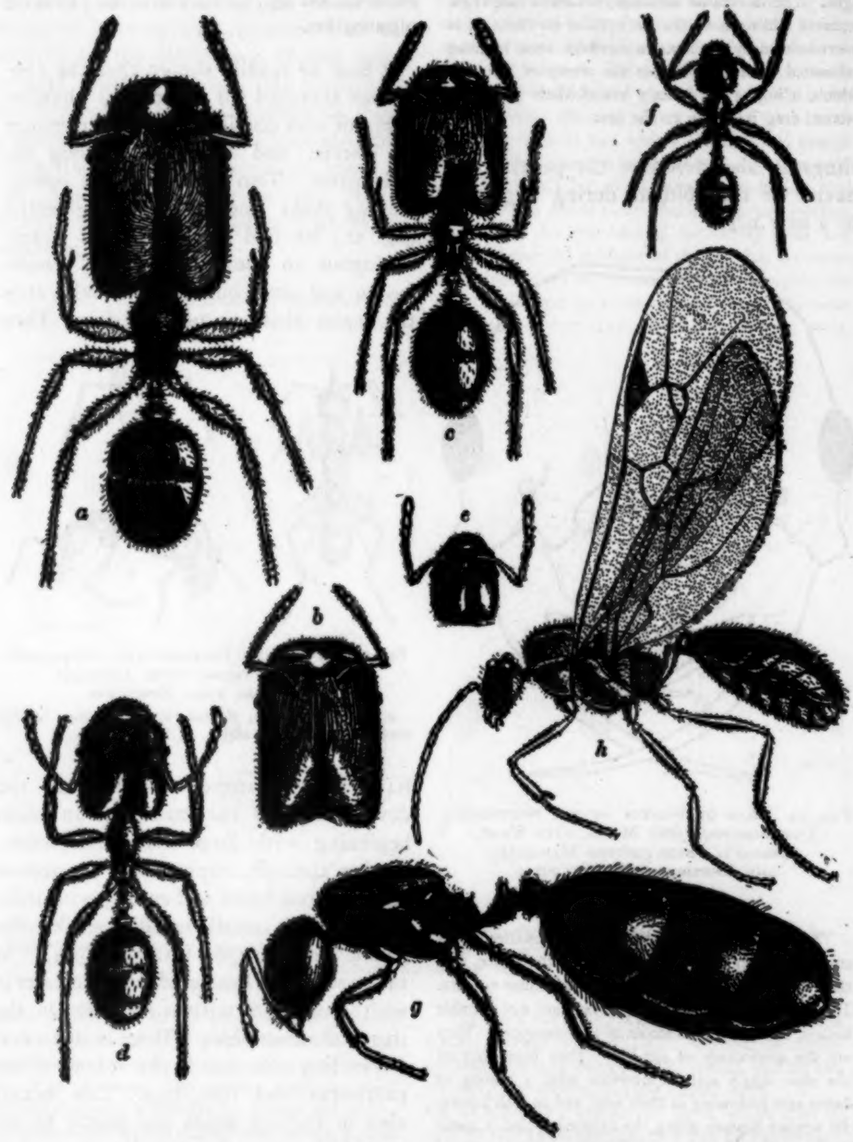

Fig. 21. Various Phases of a Small Harvesting Ant, *Pheidole instabilis*, from Texas

a, soldier; *f*, worker; *b–e*, forms intermediate between soldier and worker; *g*, female (dealated); *h*, male. All the figures are drawn to the same scale.

vided with crests or protuberances which increase the surface for the insertion of the enormous mandibular flexors and are therefore analogous to the bony crests on the skulls of many mammals that have powerful jaws and temporal muscles.

The correlation between the size and shape of the mandibles, head and prothorax is also clearly shown by a comparison of the male and female *Eupsalis minuta* (fig. 23). In the specimens figured, whose bodies behind the prothorax happen to be of the same size, you will observe that the prothorax is shorter and anteriorly narrowed in the female in correlation with the much smaller head and mandibles. The slender prolongation of the head in this sex is specially adapted for oviposition. The huge mandibles are used by the male Lucanids in their fierce sexual contests, which have been witnessed by many observers. The males of Eupsalis also fight with their mandibles, though according to Leconte and Horn (1876) their combats are bloodless and "seem, so far as the records go, to be actuated rather by chivalric sentiment, than by animal passion." According to Blatchley and Long (1916, p. 21):

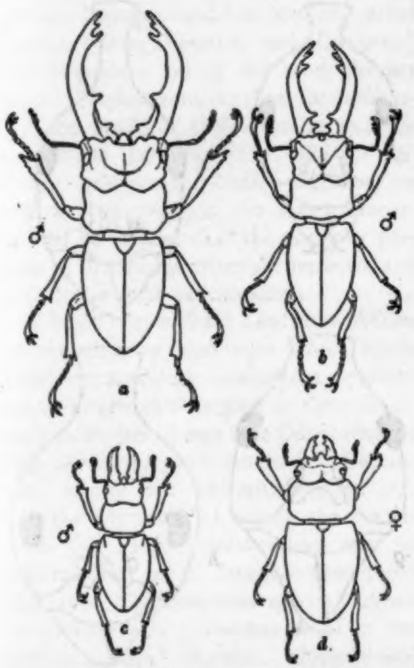

FIG. 22. FORMS OF A LUCANID BEETLE, *Metapodontus umbangi* FAIRM

a, heteromorphic male; *b*, intermediate male; *c*, homœomorphic male; *d*, female. (After Planet.)

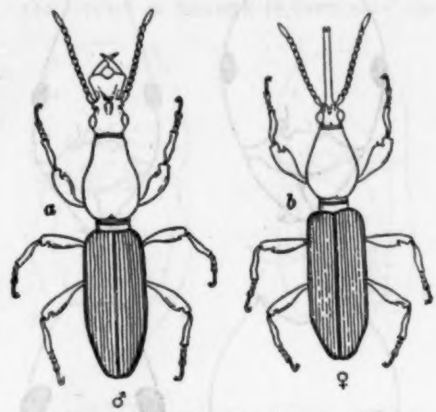

FIG. 23. A NORTH AMERICAN BRENTHID BEETLE, *Eupsalis minuta* DRURY

a, male; *b*, female

> Smith says that when the beaks of the females become wedged, as they sometimes do, the males use their forceps-like jaws to pull them out, but Riley states that the male helps in removing the beak by "stationing himself at a right angle with her body and pressing his heavy prosternum against the tip of her abdomen, her stout fore legs thus serving as a fulcrum and her long body as a lever."

After this digression I return to a consideration of some other types of heads and mandibles among the ants. Even in the smallest workers of the species hitherto described the mandibles are moderately strong and of the typical biting type, but in species that feed on

soft substances and excavate their nests in soft soil or very rotten wood or merely occupy cavities made by other insects, the mandibles may be weak and narrow and the head not only elongate and rounded behind but drawn out into a distinct neck. Among the best examples of this condition is *Apterostigma pilosum*. This ant, though related to *Atta*, does not nest in coarse ground and cut leaves but lives in cavities under bark or stones and makes its fungus gardens of insect excrement. Similar types of head (fig. 24*c*, *d*, *h*) occur in other asthenic species belonging to very different genera (*Aphaenogaster, Dolichoderus, Leptogenys, Leptomyrmex*) either as the only type among the workers or in the worker minima of species which have a large-headed soldier or worker maxima (*Dinomyrmex, Pheidole, Ischnomyrmex*).

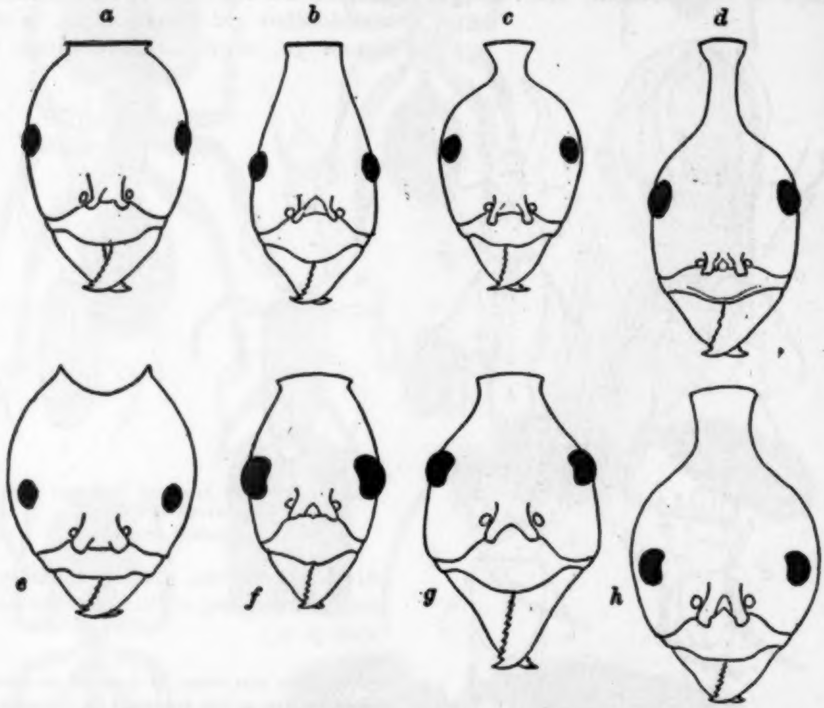

FIG. 24. PARALLEL DEVELOPMENT IN THE CONTRACTION OF THE OCCIPITAL REGION IN OLD WORLD SPECIES OF *Aphaenogaster* (*a–d*) AND NEOTROPICAL SPECIES OF *Dolichoderus* (*e–h*)

a, *Aphaenogaster* (*Nystalomyrma*) *longiceps* Sm. (Australia); *b*, *A.* (*Deromyrma*) *phillipsi* Wheeler and Mann (Palestine); *c*, *A.* (*Deromyrma*) *swammerdami* Forel (Madagascar); *d*, *A.* (*Planimyrma*) *loriai* Emery (New Guinea); *e*, *Dolichoderus decollatus* Sm.; *f*, *D. imitator* Emery; *g*, *D. rugosus* Sm.; *h*, *D. attelaboides* Fabr.

The grappling and piercing mandibles are also comparatively weak organs. The former, which are well-developed in certain Ponerinæ like the "bull-dog" ants of Australia and the species of the peculiar genus *Mystrium* are adapted for holding onto the prey while the abdomen is being bent around and the powerful sting inserted. Large hook-like mandibles

which seem to combine the functions of grappling and piercing organs are found in the soldiers of some of the army ants (*Eciton sens. str.*) (fig. 25*a*) although the next lower grade of worker (*b*) has curved, grappling mandibles and the smaller and far more abundant worker forms have cutting or biting mandibles (*c*, *d*). Both in our slave-making "amazons" of the genus *Polyergus* and in certain other genera (*Strongylognathus* and *Leptogenys*) the mandibles are of the true piercing type. The amazons use them for perforating the heads of their enemies and the species of *Leptogenys* (fig. 18*d–h*) evidently kill the soft-bodied termites, on which they prey, in the same manner. It will be noticed that the posterior portion of the head is distinctly narrowed and rounded in these various forms.

A highly specialized condition obtains in the clipping mandibles which show some extraordinary convergent developments in genera belonging to three different subfamilies of ants (the Odontomachii (fig. 16) among the Ponerinæ, the Dacetonini among the Myrmicinæ (fig. 17) and the Myrmoterini among the Formicinæ (fig. 14)). *Odontomachus* may be selected for more detailed description (fig. 16). The numerous species, known as clicking ants ("fourmis tic") in the tropics, have singular, elongate-subhexagonal heads, with the eyes placed far forward on lateral eminences while the mandibles are inserted close together at the anterior end of the head and consist of long, parallel-sided blades, with a few powerful, abruptly inflected terminal teeth and on their inner border a series of serrate denticles and long sense-hairs. The insect has a curious method of employing these organs. When it is excited they are widely opened as in the figure, and as soon as the long hairs, which act as triggers, touch an object, the blades are closed with lightning rapidity and an audible click. If during the closure their tips happen to strike against a hard body the insect is thrown off its feet and backward through the air to a distance of several inches. On opening an *Odontomachus* nest on a hot day one may hear a series of sharp clicks and find that the whole colony has suddenly evaporated into the surrounding vegetation. When the worker is hunting it cautiously approaches its insect prey with wide-open mandibles, suddenly darts forward, clips off an appendage and then retreats. It again advances and clips off another leg, antenna or wing and keeps repeating the performance till it has reduced its prey to a helpless, easily mastered torso. [For additional notes on the habits of Odontomachus see Wheeler (1900).]

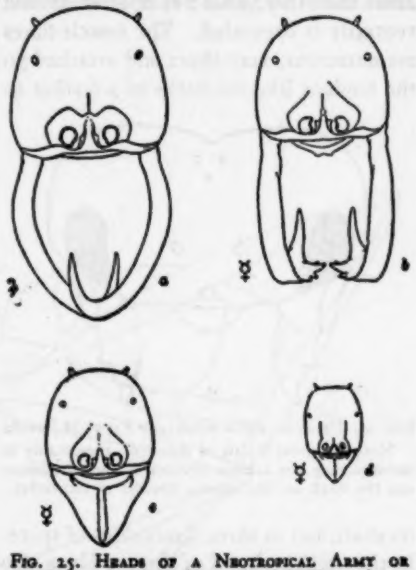

FIG. 25. HEADS OF A NEOTROPICAL ARMY OR LEGIONARY ANT (*Eciton burchelli* WESTW.)
a, soldier; *b*, form intermediate between soldier and worker; *c*, large, *d*, small worker.

In conformity with this unique behavior, the musculature of the mandibles

is peculiarly modified. The flexor mandibulæ (*fl.m.*) is very long and fills out the whole elongated posterior portion of the cranium. The tendon (*t*), attached to the swollen internal mandibular hinge, is expanded behind near the eye into a twisted, somewhat crescentic, chitinous plate (*t.pl.*) from which two long slender tendons run back very nearly to the posterior border of the head. Only one of these tendons is shown in the figure, because the other, which runs mesially and ventrally is concealed. The muscle-fibres are numerous, very short and attached to the tendons like the barbs of a feather to

FIG. 16. HEAD OF *Alysia manducator* PANZ. OF EUROPE
Note the great width of the head, presumably to accommodate the *extensor* muscles of the mandibles, and the teeth on the *external* borders of the latter.

its shaft, but in three dimensions of space. In the neighborhood of the eye fibres also run from the crescentic chitinous plate to the anterolateral walls of the cranium. Since short muscle-fibres can contract more quickly than long ones, the whole arrangement seems to be beautifully suited to closing the jaws with much greater velocity than in other ants. And the large size of the flexor muscle as a whole shows that closure is effected with considerable vigor.

The mandibles of Dacetonine ants show a bewildering variety of forms, often much like those of *Odontomachus*. Some of the species are also able to leap backward. The head, however, has a very different shape (figs. 13 and 15). It is usually more or less cordate in the worker and female, with very prominent occipital lobes and these are filled with the huge flexor mandibulæ muscles. Their fibres, in some of the species at least, are arranged along the sides of a long tendon (fig. 13). Unfortunately we possess no information in regard to the feeding habits of these ants. If we may judge from their faces they certainly do not spend their lives diffusing sweetness and light. The heads of the male Dacetonini are extraordinarily different, as will be seen from the figure of the South American *Daceton armigerum* (fig. 17). The two large drawings (*a* and *c*) represent the heads of the female and worker, the small one the head of the male (*b*). Notice the vestigial condition of the mandibles, the shortness of the cranium and the complete suppression of the great lobes which in the other castes contain the flexor muscles of the mandibles. Owing to these deficiencies the countenance of the male wears a very meek and vacuous expression compared with the satanic countenances of the female phases.

Among the ants with aberrant types of mandibles I will select only two. In one of them, *Thaumatomyrmex* (fig. 19), of which only a couple of tropical American species are known, each mandible is split into three long slender spines. The narrowing and rounding of the posterior portion of the head indicates that the flexor muscles must be very feeble. We know nothing of the habits of these insects, only a few, isolated specimens of which have ever been taken. Perhaps they feed on very soft-bodied larvæ or small snails in which case the mandibles might be used for puncturing the integument of the prey in several places. The other type is that of *Harpegnathos*, an

East Indian ant with extraordinary mandibles known to be employed in leaping (fig. 20). The insect apparently bends its head completely under the body, presses the tips of the mandibles against the ground and by suddenly raising its head, leaps forward to a distance of a yard or more. This habit, however, does not completely account for the unusual conformation of the mandibular blades, especially of their large basal teeth (Wheeler, 1922).

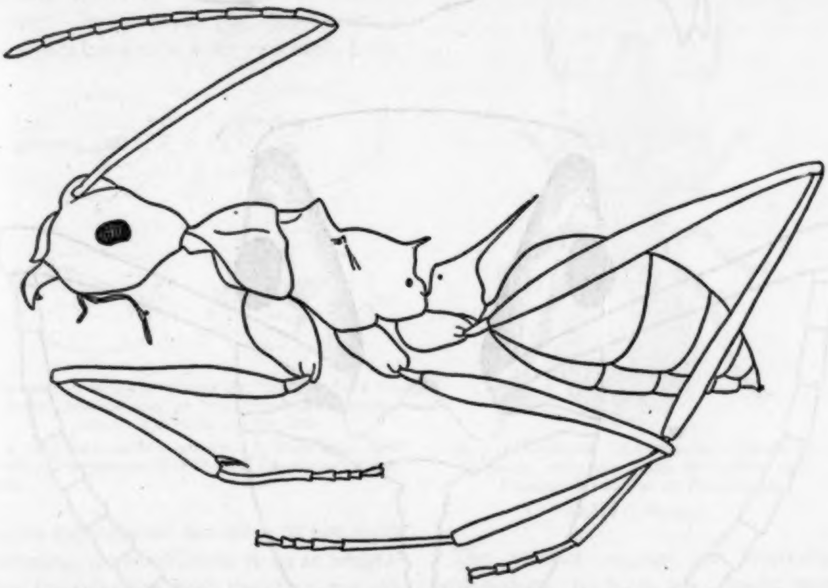

FIG. 27. *Polyrhachis (Myrmatopa) ulysses* FOREL FROM THE SOLOMON ISLANDS; WORKER IN PROFILE, SHOWING CONVEXITY OF THE FRONT

Much of what I have said about the mandibles of ants, their musculature and the shape of the head will, I believe, hold good of many other mandibulate insects. Professor C. T. Brues, however, calls my attention to two unrelated groups of Parasitic Hymenoptera, the Alysiidæ and Vanhorniidæ, in which the function of the mandibles and probably also the development of their musculature are reversed. In the accompanying outline figure of the head of *Alysia manducator* (fig. 26) it will be observed that the mandibles have the teeth on their external instead of their internal borders. Obviously in this case the extensor muscles have much more work to perform than the flexors and are therefore probably larger. This is indicated by the unusual width of the head and the distance between the eyes. Of course, such exodont mandibles cannot be used for biting or mastication, but might be employed by the insect in forcing its way through soft wood, mushroom-tissues, etc. We unfortunately possess no observations on the habits of the Alysiidæ beyond the fact that their larvæ live in the larvæ of various Diptera, Coleoptera and Lepidoptera.

The heads of ants vary considerably in the convexity of their dorsal surface. As a rule, they are most convex in the region

of the vertex and occiput, a condition which is, of course, correlated with the development of the flexores mandibulæ already described, but in a few genera due to the greater development of the flexor and extensor antennal muscles, which run from the articulations of the appendages downward, backward and

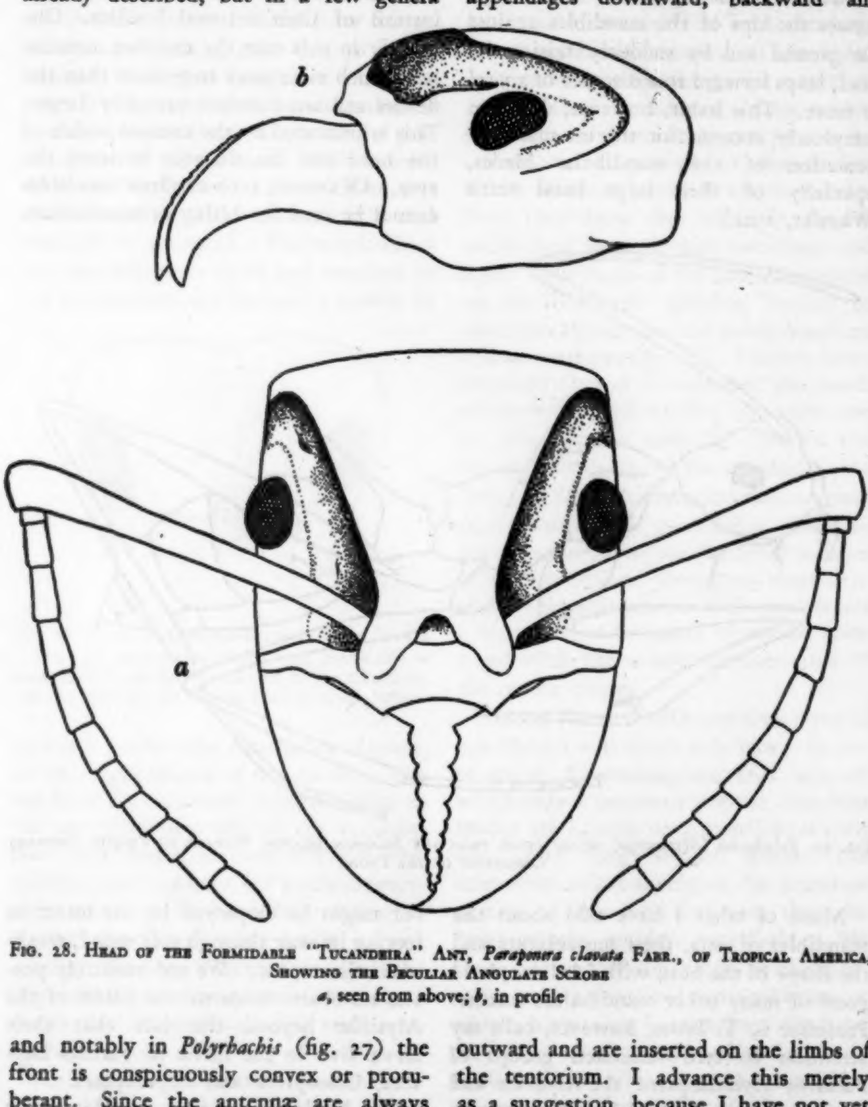

FIG. 28. HEAD OF THE FORMIDABLE "TUCANDEIRA" ANT, *Paraponera clavata* FABR., OF TROPICAL AMERICA, SHOWING THE PECULIAR ANGULATE SCROBE

a, seen from above; *b*, in profile

and notably in *Polyrhachis* (fig. 27) the front is conspicuously convex or protuberant. Since the antennæ are always long and very mobile in such insects I believe that the frontal convexity must be outward and are inserted on the limbs of the tentorium. I advance this merely as a suggestion, because I have not yet had an opportunity to study the anatomy of *Polyrhachis*.

DEVELOPMENT OF GROOVES FOR ANTENNÆ

The sides of the head in ants are sometimes peculiarly modified by the development of grooves, or scrobes for the partial or complete concealment of the antennæ. In their simplest form, e.g. in many species of *Pheidole*, *Harpagoxenus* and *Tetramorium*, these scrobes are formed by a backward prolongation of the frontal carinæ and a longitudinal depression of the adjacent cranial surfaces. In certain other genera, however, the grooves become deeper. In *Paraponera* (fig. 28) we find a very peculiar scrobe with two limbs form-

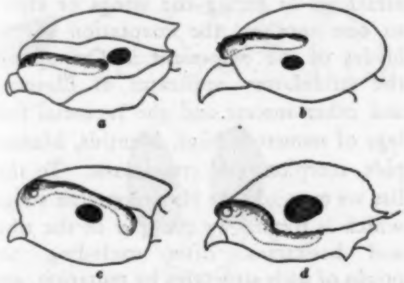

FIG. 29. PROFILES OF HEADS OF VARIOUS ANTS TO SHOW DEVELOPMENT OF THE ANTENNAL SCROBE AND ITS RELATION TO THE EYE

a, *Cryptocerus multispinus* Sm.; *b*, *Meranoplus mars* Forel; *c*, *Procryptocerus belti* Forel; *d*, *Cataulacus erinaceus* Stitz

ing an angle around the eye. At first sight this structure would seem to be an adaptation for receiving both the scape and the flagellum of the antenna, but the scape and flagellum are really too long to form an angle that will fit into the scrobe. Hence the dorsal limb can accommodate only the basal portion of the scape when it is folded back and the ventral limb only the tip of the flagellum. In *Paranomopone* the scrobe is divided near the middle by a slender partition into two grooves one of which accommodates the scape, the other the flagellum. In still other genera the scrobe is simple but sufficiently deep to receive the whole folded antenna or at any rate the whole scape (fig. 29). In *Cryptocerus* (*a*) the scrobe lies in front of the eye, in *Procryptocerus* and *Meranoplus* (*b* and *c*) it runs backward over the eye, in *Cataulacus* (*d*) it descends below the eye. In all of these genera, and especially in *Cryptocerus*, the frontal carinæ may be greatly expanded laterally, so that the head becomes very broad and shield-shaped, with plate-like lateral margins (fig. 30).

FIG. 30. *Cryptocerus* (*Zacryptocerus*) *clypeatus* F.; WORKER, WITH THE HEAD BROADENED AND FLATTENED FOR USE IN PHRAGMOSIS

(After C. Emery)

The scrobes suggest an interesting evolutionary problem. It would seem that they might be formed in the pupa by the pressure of the antennæ against the still soft and plastic cranial integument, but when we examine the young pupæ of the various genera I have mentioned, we find that the antennæ are not folded up against the sides of the head but are drawn down over the ventral surface of the legs as in the pupæ of many other insects. The scrobes therefore develop independently during the ontogeny and we are compelled to conclude that

these grooves, so beautifully adapted in the adult to the reception and protection of the very sensitive and important antennæ, must have arisen during the phylogeny of the various species in which they occur. The notion that they were produced by natural selection may be dismissed as improbable for the simple reason that they cannot have had survival value, because they are altogether lacking in most of the larger and more dominant genera (*Monomorium*, *Crematogaster*, *Polyrhachis*, *Formica*, most *Camponotus*, etc.). The only hypotheses, it seems to me, that might be advanced to account for the scrobes are those that have been discussed in connection with many similar cases of functionally correlated structures, namely, first, the Lamarckian hypothesis that habitual pressure of the antennæ against the hard integument of the adult cranium has affected the germplasm in such a manner as to lead to the gradual development of scrobes in the pupal offspring of succeeding generations, and second, the mutation hypothesis of the chance, spontaneous origin of scrobe-producing genes in the germplasm. The latter hypothesis fails to account for the highly adaptive character of the scrobes and the former labors, of course, under the difficulty of explaining how the habitual pressure of the antennæ against the hard, unyielding cranial cuticula of the adult could translate itself into a definite formative, or morphogenic tendency in the individuals of succeeding generations.

PROBLEMS OF ADAPTATION

A number of exquisite structures similar to those here described have been discussed by Cuénot (1925) in his very interesting little book on adaptation under the head of "coaptations." These he defines as "reciprocal adjustments of two independent parts analogous to that formed by the blade fitting into the handle-groove of a pocket-knife, or a button into its button-hole." As examples he cites the fore legs of certain Phasmids which are curiously bent at the bases of the femora to fit around the head, a case originally described by Stockard (1909), the pressure-button (used on gloves and invented in France about 1886), shown in the two attachments of the mantle in cuttle-fishes and the attachment of the hemielytra to the thorax in numerous aquatic Hemiptera, or Hydrocorisa (*Ranatra*, *Belostoma*, *Notonecta*, *Naucoris*, etc.), the devices in many insects for attaching or fitting the wings or elytra to one another, the coaptation of the blades of the ovipositor in Orthoptera, the stridulatory apparatus of Elaterids and other insects and the raptorial fore legs of numerous bugs, Mantids, Mantispids, scorpions and crustaceans. To this list we may add the Hymenopteran strigil which is formed by the spur of the tibia and basitarsus. After excluding the origin of such structures by mutation, and omitting all mention of the Lamarckian hypothesis, Cuénot says:

> Without a doubt, coaptation is the end-stage of a *directed* evolution. Sufficient indications of this evolution are known to permit its affirmation. There are Phasganourids with short ovipositors which have gutters that are rather imperfect though adequate for the movements of oviposition. There are, foreshadowing the saltatory apparatus of Elaterids, certain imperfect conformations of a similar type; the *Corixas* have an apparatus simpler and less compact than the pressure-button of other aquatic Hemiptera, many predatory insects have ambulatory legs which serve equally well for seizing the prey though not of the highly differentiated type of the specialized raptorial legs in the Mantids and Naucorids. Now the only directing agency we know is Darwinian selection. This would have to play the rôle of a handicraftsman gradually correcting and perfecting his work, successively and tentatively, till it attained a complete and definitive functional specialization which could not be surpassed. Even admitting the omnipotence of natural selection, however, it could

not create the coördinated details of the coaptations, and it is just the origin of these details we find so difficult to understand. And then how improbable it is that the elytral apparatus of a *Lucanus*, the spur of the raptorial legs of a *Ranatra*, the stridulatory raspof a longicorn, can have had sufficient vital importance during their incipient stages to have brought about differential extinction! But after these negations, nothing remains. It would be pure metaphysical amusement to imagine within the species a meticulous and fanciful demon, a regulator and director of mutations, even if he were decorated, as he has been by some, with such pompous epithets as "internal perfective tendency," "élan vital," "entelechy," or some other term. Again we must resign ourselves to saying: *ignoramus!*

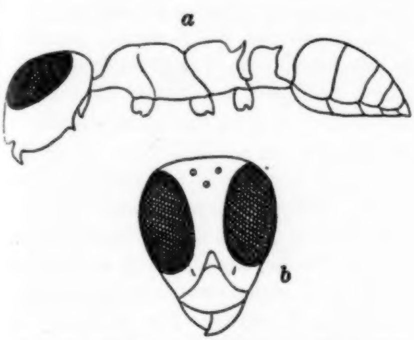

FIG. 31. *Santschiella kohli* FOREL; A HUGE-EYED FORMICINE ANT FROM THE CONGO

a, worker in profile; *b*, head of same from above. (After Forel.)

DEVELOPMENT OF EYES

Much might be said about the physiognomic significance of the eyes of ants and other insects, but the space allotted to this article and the reader's patience are limited, and I must be brief. In nearly all male Formicidæ, of course, the eyes are very large, but this is true of the females and workers only in a few rather primitive and archaic genera. The facial expression of these macrophthalmic forms is very unlike that of other ants. Thus *Santschiella* (fig. 31), which is known only from a single worker specimen taken in the Belgian Congo looks as if it were

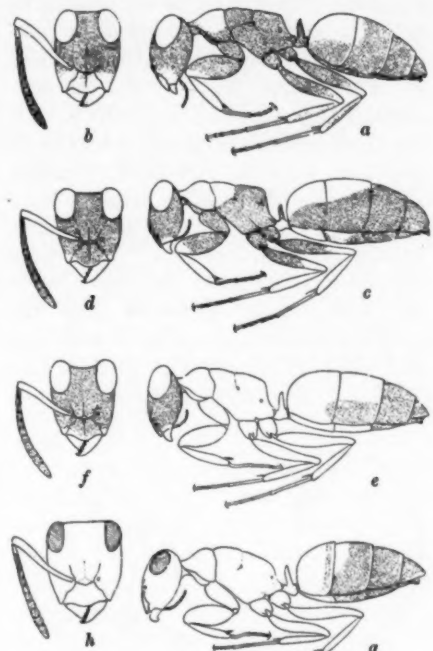

FIG. 32. WORKERS OF FOUR SPECIES OF THE LARGE-EYED AUSTRALIAN GENUS *Opisthopsis*

a and *b*, *O. respiciens* Sm.; *c* and *d*, *O. pictus* Emery var. *lepidus* Wheeler; *e* and *f*, *O. rufithorax* Emery; *g* and *h*, *O. major* Forel.

FIG. 33. A LARGE-EYED LEAPING ANT, *Gigantiops destructor* FROM BRITISH GUIANA

Dorsal and lateral view of worker and head seen from above.

hopelessly flabbergasted by the problem of existence and therefore resigned to race-suicide, and the species of the Australian genus *Opisthopsis* (fig. 32) and the neotropical *Gigantiops* (fig. 33), which have the large eyes at the posterior corners of the head, wear the expression of pained astonishment which as children we have all seen on the face of some school-marm or elderly maiden relative. It is more difficult to characterize the expression of the East Indian *Myrmoteras* (fig. 14) with its unique combination of huge eyes and clipping mandibles. If there are Anthony Comstocks, movie censors and

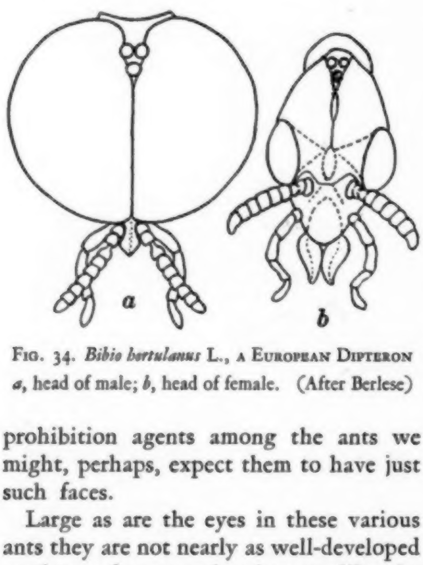

Fig. 34. *Bibio hortulanus* L., a European Dipteron
a, head of male; *b*, head of female. (After Berlese)

prohibition agents among the ants we might, perhaps, expect them to have just such faces.

Large as are the eyes in these various ants they are not nearly as well-developed as those of many other insects, like the Diptera, Lepidoptera, Odonata, many Hemiptera, etc. In most of these orders, however, the mandibles are poorly developed or reduced to stylet-like appendages. In many male Diptera the eyes form nearly the whole head. An instructive case is furnished by *Bibio* (fig. 34) in which this condition is seen in the male, while the female has very small eyes and a very different head, narrowed and rounded behind like that of certain ants (*Lobopelta*) with poorly developed mandibles.

BEARDED ANTS

Of course, the physiognomy of ants is also determined to some extent by the character of the sculpture and pilosity. The sculpture, especially when it assumes the form of rugæ or reticulations is sometimes strangely suggestive of the wrinkles in the aged human countenance (*Diacamma*, some species of *Pheidole*, etc.). The various coiffures and styles of moustaches, whiskers and eyebrows are often extraordinary, but I will not dwell on them, because I might be tempted to depart too far from the arctic dignity so becoming to an entomologist. Nevertheless there is one type of beard to which I must call attention, because it has a very precise and practical function, unlike the human beard, which is supposed to have a great variety of functions—aesthetic, honorific, bacteriologic (or rather bacteriolegic), camouflagic, calorific, or merely problematic. And whereas in the human species it is the peculiar prerogative of the male to wear this form of pilosity, among the ants it is—*horribile dictu*—the females, i.e., the queens and workers that insist on cultivating it. But such improper customs prevail only among the species that live in deserts. Some years ago I discussed these ants in a tonsorial paper which might have attracted more attention had it been published in some barber's monthly instead of the Biological Bulletin (Wheeler, 1907).

Among the dominant ants of the arid, desert regions of the globe there are a number of species belonging to several genera and no less than three of the seven natural subfamilies (Myrmicinæ, Dolichoderinæ and Formicinæ) which have

series of conspicuously long, curved hairs on the chin (gula), mandibles, and clypeus (fig. 35). The arrangement of these hairs which form a kind of crate is most typical and most like that of the old-fashioned Irishman's chin-whiskers in the large Western harvesting ants of the genera *Pogonomyrmex* (fig. 35*a*) and *Veromessor*, and of the genus *Messor*, which ranges over the dryer parts of Africa,

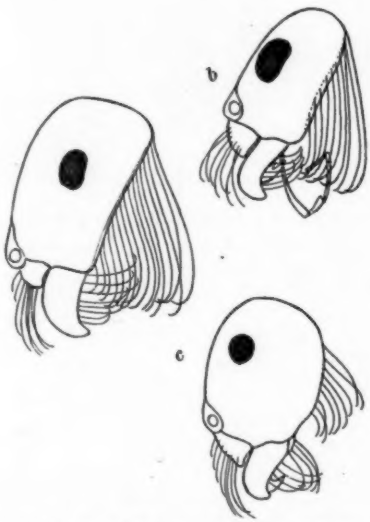

FIG. 35. HEADS OF DESERTICOLOUS ANTS IN PROFILE TO SHOW DEVELOPMENT OF THE PSAMMOPHORE IN THREE DIFFERENT SUBFAMILIES

a, *Pogonomyrmex californicus* from Southern California (Myrmicine); *b*, *Dorymyrmex* (*Psammomyrma*) *planidens* from Argentina (Dolichoderine); *c*, *Melophorus bagoti* from Central Australia (Formicine).

southern Europe, and Central Asia. Similar hairs are also developed in the deserticolous species of *Monomorium*, *Dorymyrmex* (fig. 35*b*), *Melophorus* (fig. 35*c*), *Cataglyphis*, *Myrmecocystus*, and *Camponotus*. Santschi (1909) has shown that the gular crate, which he calls the "psammophore," is used as a basket in which to carry the sand and dust to the surface while the insects are excavating their burrows. Without such equipment the species nesting in dry sand or earth would probably find excavation extremely laborious and time-consuming, because the mandibles are not suited to the transportation of very finely-divided or powdery substances.

Besides the psammophore just described there are in certain ants other more important modifications of the head that may be interpreted as adaptations to the non-living environment. The most conspicuous of these have evidently developed in response to the habitual contacts of the insects with the walls of their burrows, especially when they are tubular and excavated in solid wood. Similar and even more striking cases are well-known among both larval and adult beetles, notably among the Ipidæ, Platypodidæ, Bostrichidæ, Ptindæ, Cerambycidæ, etc. The insect, especially if it rotates while boring through the wood, makes a perfectly tubular gallery, in adaptation to which the body takes on a more or less perfectly cylindrical form. But since most ants, even many of the wood-boring species, have rather long, slender bodies, they need to acquire no special adaptive change in structure, though in some tropical species, and especially in the queens, the tenuity of the body may be greatly exaggerated. This is the case, e.g., in the Myrmicine *Pseudomyrma filiformis* (fig. 36) which, according to my observations, regularly inhabits the very narrow pith-cavities of a particular neotropical shrub. And in *Camponotus* (*Myrmostenus*) *mirabilis* (fig. 37) which belongs to a different subfamily, the Formicinæ, we find a very similar elongation of the head and body. The latter species is known only from single female specimens taken at lights, but there can be little doubt that its nesting habits are much like those of *Ps. filiformis*.

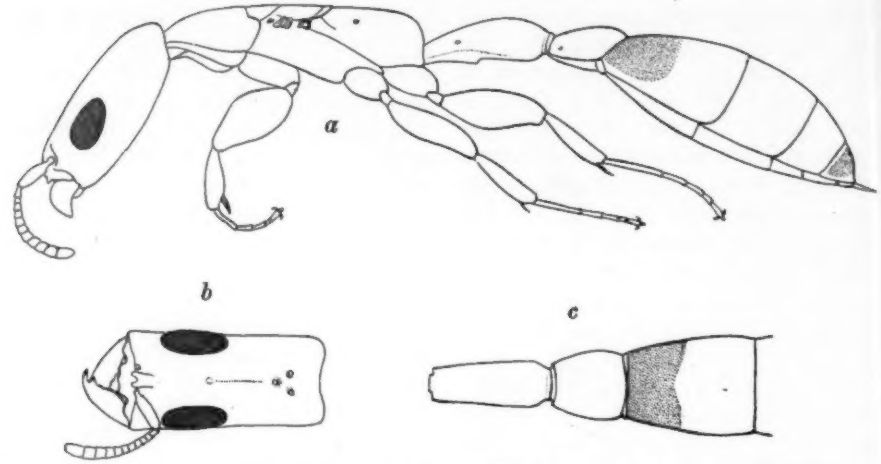

Fig. 36. A Neotropical Pseudomyrmine Ant, *Pseudomyrma filiformis* Fabr., Adapted to Living in Hollow Twigs

a, female (deälated) in profile; *b*, head of same from above; *c*, pedicel and first gastric segment from above

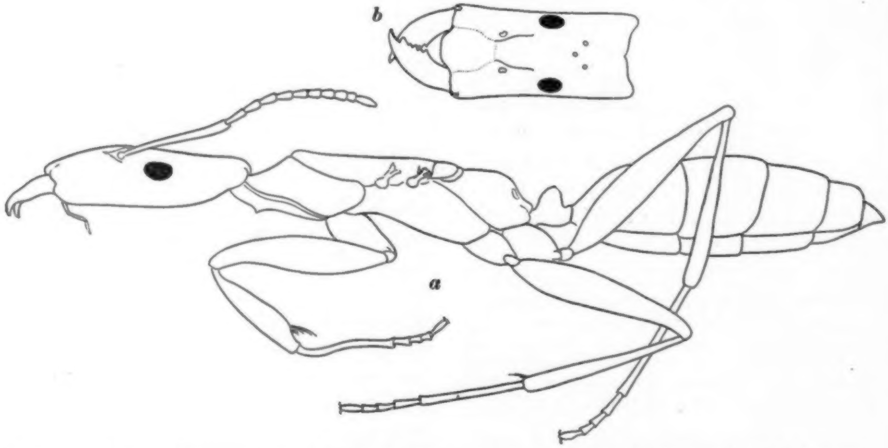

Fig. 37. *a*, Female (Dealated) of a Peruvian Formicine Ant, *Camponotus (Myrmostenus) mirabilis* Emery, Adapted to Life in Hollow Twigs; *b*, Head of Same from Above

PHRAGMOSIS

A more interesting adaptation to living in hard-walled, tubular cavities occurs in several genera, e.g., *Camponotus*, whose queens and soldiers have short, cylindrical and anteriorly sharply truncated heads, with the truncated surface circular, indurated and more strongly sculptured than the remainder of the body (fig. 38). These ants use the head, like the thick door of a safe, to close the entrance of the nest and keep out intruders. The nest which is excavated in hard wood, lig-

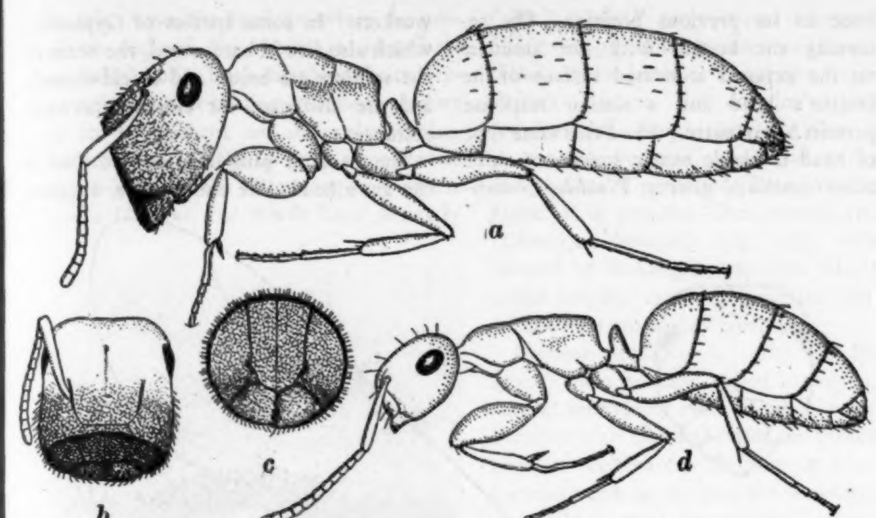

FIG. 38. *Camponotus (Colobopsis) etiolatus* WHEELER, A COMMON PHRAGMOTIC ANT IN THE LIVE OAK GALLS OF TEXAS

a, soldier; *b*, head of soldier from above; *c*, same directly from front; *d*, worker

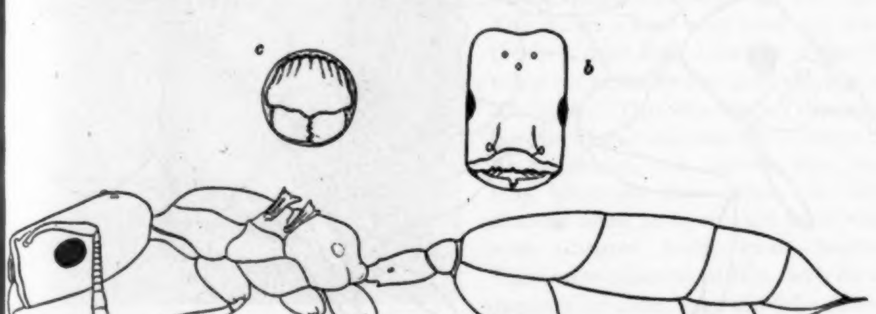

FIG. 39. *Crematogaster (Colobocrema* SUBGEN. NOV.) *cylindriceps* SP. NOV., A PHRAGMOTIC TWIG-INHABITING ANT FROM THE PHILIPPINES

a, female (deälated) in profile; *b*, head from above; *c*, anterior view of head

neous galls or the stems of rushes, has a perfectly circular entrance which is guarded by a soldier whose head exactly fits the orifice. When a worker desires to forage she strokes the soldier's abdomen with her antennæ and the animated door moves back and as soon as she has passed out of the nest returns at

once to its previous position. On returning she knocks with her antennæ on the exposed truncated surface of the janitor's head and a similar response permits her to enter. I find this same type of head in single exotic species of three other unrelated genera: *Pheidole*, *Cremato-*workers. In some species of *Cryptocerus*, which also live in hard wood, the heads of the soldiers are broad and shield-shaped, and are also used for closing the nest-entrances.

The peculiar plug-like modification of the ant's head, like the scrobes, suggests

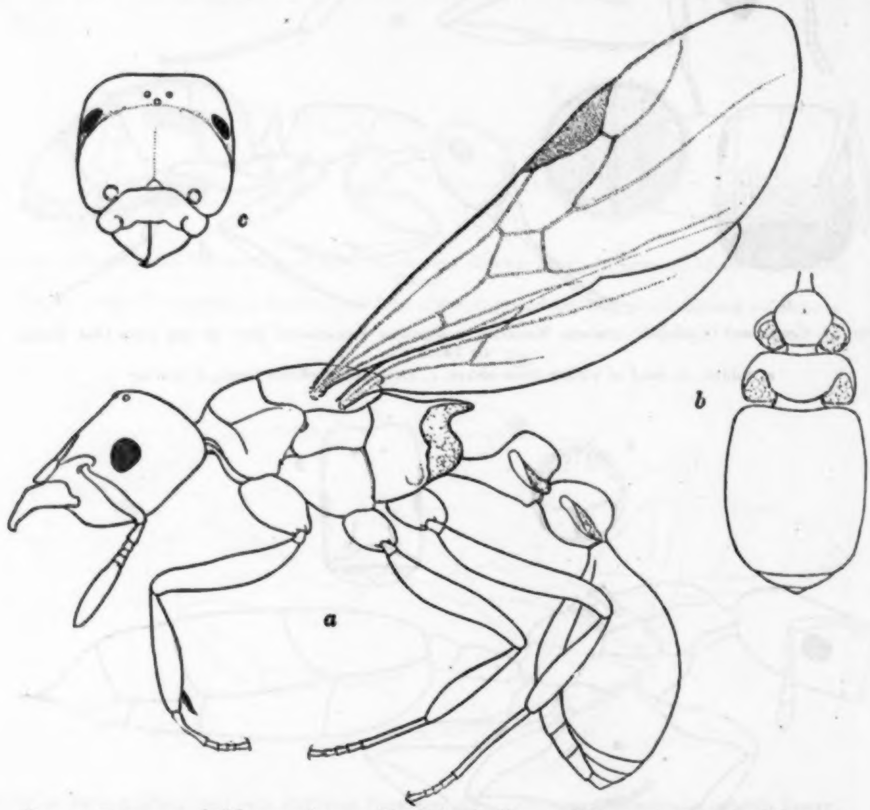

FIG. 40. *Epopostruma* (*Colobostruma* SUBGEN. NOV.) *lea* SP. NOV., A PHRAGMOTIC ANT FROM AUSTRALIA
a, female in profile; *b*, pedicel and gaster; *c*, head from above

gaster (fig. 39), and *Epopostruma* (fig. 40), which, in all probability have much the same habits. There are also several lignicolous subgenera of *Camponotus* (*Paracolobopsis*, *Pseudocolobopsis*, *Manniella*, *Neomyrmamblys*) which exhibit similar modifications of the head in the queens and major an interesting problem which can be briefly discussed in this place. Very similar adaptations for closing the entrances to the burrows are found not only in a number of other Arthropods (e.g., in the termites of the genus *Cryptotermes*) but also in animals belonging to other phyla.

In some cases the head, in others the posterior end of the body is adaptively modified, but in both instances the truncation, its circular outline and the hardening of its integument are strangely similar. Sometimes, as in the larvæ of tiger-beetles (*Cicindela*) and the burrowing bees of the genus *Halictus*, the whole head is nearly

Fig. 41. A Toad, *Bufo empusus* from Cuba, Which Closes Its Earthen Burrow with Its Hard, Shelly Head
(After T. Barbour)

circular and plug-shaped, in other forms, like the bark-beetles (Scolytidæ, Platypodidæ) and the caterpillars of *Circinnus melshaemeri* and *Perophora sanguinolenta* which inhabit tubular cases made of leaves, the posterior end of the body is sharply truncated and roughened or spinulate. A figure and description of the habits of *C. melshaemeri* is given in Harris (1862), while *P. sanguinolenta* is figured in Sharp (1899). I have observed the caterpillars of the latter or an allied species in British Guiana. In certain Annelids (Maldanidæ, Amphictenidæ) that live in tubular burrows, the head is hard and shelly. I reproduce Petrunkevitch's figure of a peculiar Theraphosid spider (*Chorizops loricatus*) (fig. 42) which, instead of making a trap-door like the allied species, uses the posterior end of its body for closing its burrow.

Barbour (1914, 1919, 1926) and Dunn (1926) have recently called attention to several interesting cases of the closure of burrows with modified heads and posterior ends in vertebrates. Barbour in his delightful book on reptiles and amphibians says: "It is well known that in many frogs the skin of the head becomes involved in the cranial ossification and becomes adherent, indurated, and rugose. This makes a hard bony head and should the frog back into a burrow it has but to tip his head down to close the entrance effectively. That this was ever regularly done on a large scale was never known until by chance, the author, after many long hunts for *Bufo empusus* in Cuba, chanced upon an open field over which were scattered many small burrows. These were evidently of two sorts, for the openings of some were carefully rimmed with smooth patted clay, while the others were rough and looked unfinished. Each of those with the rims contained one of the toads for which he had searched so long—the *sapo de concha* in Spanish—the shell-headed toad. These tube-like burrows were perfectly cylindrical, and perhaps seven to ten inches deep. The toad, which always looked larger than the burrow, when it was removed, was to be found near the bottom of the hole, the horn-like head forming a perfect operculum and perfectly fitting the caliber of the

tube." With Dr. Barbour's permission I reproduce his figure of this toad (fig. 41). Both he and Dunn have shown that a very similar closure of the burrow occurs in a number of wood inhabiting tree-frogs (e.g. in *Hyla lichenata* of Jamaica). In this connection Barbour also calls attention to two other groups of vertebrates in which the posterior end of the body is similarly employed, namely the snakes of the family Uropeltidæ, "where the head is sharp and the tail knobbed and shielded off and is covered by a bony shield. This closes the burrow perfectly and no prying snake following its underground path could possibly get its jaws about it."

As there is no general term to cover all the peculiar, sporadic but convergent modifications of the ends of the body for closing tubular burrows I suggest the word "phragmosis," from φραγμός, a fence or barricade. From evolutionary and behavioristic points of view the phenomenon, as one of the most striking and

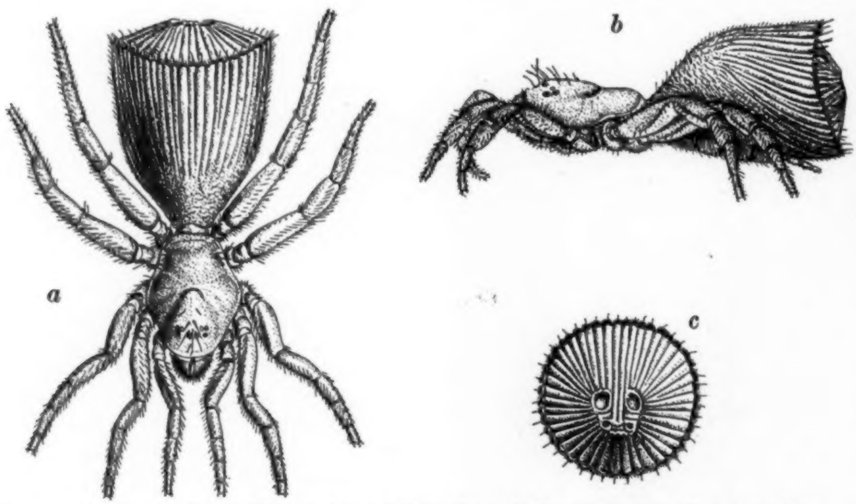

FIG. 42. A NEOTROPICAL SPIDER (*Chorizops loricatus*) WHICH CLOSES ITS BURROW WITH THE TRUNCATED POSTERIOR END OF ITS ABDOMEN

a, dorsal view; *b*, lateral view; *c*, truncated surface of abdomen. (After A. Petrunkevitch)

or even sometimes roughened," and certain small armadillos, of which he says: "Perhaps the most marvelous example of all is to be seen among mammals, in the two species of Pichiciegos of Bolivia and northwestern Argentine. These little armadillos of the genus Chlamydophorus burrow and live underground. Their body is nearly cylindrical, the head sharp and pointed, and the great fore limbs are mole-like in the extreme, but the posterior end of the body is as if sharply chopped

definite methods of protection and defence, would seem to deserve more careful investigation than it has received. The phragmotic insect, instead of secreting or constructing a stopper, like the operculum or epiphragm of snails and the earthen or silken barricades or doors erected at the entrances of their burrows by many ants, wasps and trap-door spiders, actually employs for the purpose a specialized portion of its own body, thus affording a proof that no hard and fast line can be drawn

between behavioristic activities on the one hand and physiological and morphogenic processes on the other. The phylogenetic development of phragmosis is obscure. The ants, at least, seem to indicate that it cannot have arisen as a sudden, saltatory variation, but must have developed gradually, since we have among the many species of lignicolous *Camponoti* continuous series of approximations to the perfected condition observed in *Colobopsis* (fig. 38).

DETERMINATION OF SHAPE OF THORAX AND ABDOMEN

It will be seen from the foregoing discussion that the most important general factor in determining the shape and size of the head, at any rate in insects with biting mouthparts, is the flexor musculature of the mandibles. When we turn to the great motor region of the insect body, the thorax, the dependence of the size and shape of the skeleton on the volume of the leg and especially of the wing musculature, becomes even more manifest. Attention has been so often directed to this matter, that little remains to be said about it. Such insects as the aphids show the correlation very clearly during their post-embryonic instars, but the various castes even of a single species of ant, furnish an even more impressive illustration. In worker ants, which never develop wings, save as rare, pathological vestiges, the thorax is greatly simplified in structure and diminished in size as compared with the thorax of the winged castes; and among the queens of certain species (*Leptothorax emersoni*) we discern a gradual reduction in its size and complexity as we pass from the macrothoracic, winged individuals, through steno- to microthoracic, apterous forms essentially like the workers. That the development of the wing-muscles very largely determines the size and shape of the thorax is also revealed by a comparative study of insects like the Odonata, Hymenoptera, Diptera and Coleoptera, in which the relative volumes of the meso- and metathoracic segments are clearly correlated with the relative size and efficiency of their respective pairs of wings.

The physiognomy of the insect abdomen, however, is not determined so much by the development of the musculature of the various segments as by the volume of the viscera, i.e., the alimentary canal, reproductive organs and fat-body. The phenomenon of "physogastry," or hypertrophy of the abdomen is in some cases due to an enormous increase in the contents of the crop, as in the honey-ants, in others to enlargement of the ovaries or fat-body, as in the aged queens of termites and certain ants (*Dorylinæ*, *Anergates*) and the various termitophiles of the more extreme type (*Corotoca*, *Spirachtha*, etc.). This physogastry is really of considerable physiological interest but its adequate consideration would unduly expand this article.

In conclusion we may revert briefly to some of the general types observed in man—the dysplastics, giants, dwarfs and acromegalics. Stockard has shown that very similar types may be clearly recognized among the various breeds of dogs, such as the St. Bernard (acromegalic), bull-dog (achondroplastic dwarf), black-and-tan (ateleotic dwarf), etc. Many cases of giantism and nanism might be cited among the insects, and among the dwarfs the soldiers of certain ants (*Pheidole*, *Acanthomyrmex*, etc.) are in many respects strangely analogous to the achondroplastics (fig. 21*a*), while the small workers (fig. 21*f*) are even more like the ateleotics. The development of these forms evidently depends on both genetic

and endocrine factors but the proportional intervention and interrelation of these factors have not been established. Owing to lack of knowledge of the precise functions of the various glands which in insects might be regarded as analogous to the endocrine glands of vertebrates, we are unable to frame any satisfactory physiological explanation of the Hexapod dwarfs. If certain ants have really learned to produce achondroplastics and ateleotics *ad libitum* and to turn over to them the main asexual activities of the colony, we should have another fine example of the extraordinary ability of insects to exploit to the utmost everything in their environment. As yet man has learned to employ his achondroplastics, ateleotics and other dysplastics only as court pets, court jesters and circus freaks.

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ANTHROPOID BEHAVIOR

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INTRODUCTION

IN THE first quarter of the present century both scientific and popular interest in the anthropoid apes has increased steadily and greatly. Publications have multiplied correspondingly. Despite lively interest in other primates, and in other phenomena than those of behavior, we have been constrained by the magnitude of our task and the space allotted us to limit this digest to studies of the behavior and mentality of the four existing types of anthropoid ape: the gibbon, the orang-utan, the chimpanzee, and the gorilla. For convenience we shall hereafter use the term ape as synonymous with anthropoid ape.

Morphologic, taxonomic, and physiologic publications, however intimately related to psycho-biological problems, have been omitted unless they contain significant original contributions to behavior. As our primary recent sources of aid in matters of classification, structure, and genetic relations, we have used the pertinent works of Elliot (28) and Sonntag (72). The former, in addition to taxonomic information, supplies an immense amount of miscellaneous material on the habits and life-history of the apes, and the latter, with his convenient summary of their morphological characteristics, supplies a bibliography of over five hundred titles. Although many authors consider anthropoid characters, discussions of evolution have been omitted from this digest because they give but scant and inexpert attention to psycho-biological phenomena.

The chronological limits of our survey were dictated by the beginnings in 1912 of determined endeavor to provide facilities for anthropoid research, and by the date of writing—March, 1926. Prior to 1912 no major experimental contribution to our knowledge of the behavior of an anthropoid ape had been published.

Although it necessitates slight repetition of references, topical arrangement of materials has been employed and generally under topics the chronological order. Popular papers have been ignored, except in those few instances in which they present original observations. Ordinarily, we have excluded also preliminary announcements, summaries, and abstracts. Aside from these intentional omissions the bibliographic list is thought to be reasonably complete.

HISTORY OF ATTEMPTS TO PROVIDE FOR ANTHROPOID RESEARCH

In 1912 appeared the first account of a plan for an anthropoid station on Tenerife, the Canary Islands. It originated apparently with Professors Rothmann and Waldeyer in Berlin (62, 63, 74, 75). Rothmann's publications fully describe the project. Dr. E. Teuber, a young German psychologist, was the first resident investigator. His period of residence was short and but one publication (64) reports his work. His successor,

Dr. W. Köhler, continued in residence at the station for several years conducting psycho-biological investigations. During the World War he was virtually interned on Tenerife and lacked scientific resources and contacts essential to the satisfactory conduct of his work. Following the war the Canary Island Anthropoid Station was discontinued because of lack of funds for its maintenance; Dr. Köhler returned to Germany, and the survivors among the chimpanzees which had served as his subjects were transferred to the Berlin Zoölogical Garden.

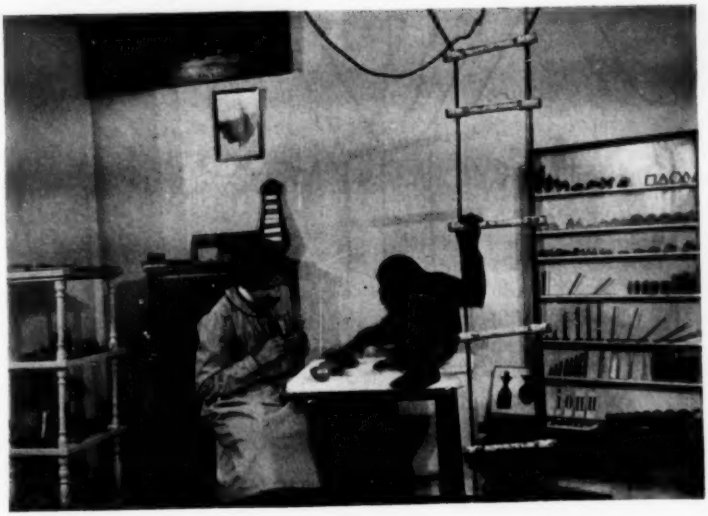
The German station was established primarily to afford opportunity for studies in structural and functional neurology, but the experimental work actually conducted there during the six or seven years of its existence was psycho-biological and concerned almost wholly with problems of anthropoid behavior. It is one of the major tragedies of biological science that this initial effort to make excellent provision for the scientific study of the apes should have failed from lack of funds.

Simultaneously with the fostering and expression of interest in anthropoid research in Berlin, similar interest gained expression in the United States in the activities of Hamilton in California and Yerkes in Harvard University. The former for several years maintained at Santa Barbara, California, a small colony of monkeys and apes in which he studied various psycho-physiological problems, with special reference to his professional interest in psychopathology. Subsequently, the Hamilton colony was used by Yerkes in an experimental study of ideational behavior. Both colony and laboratory were abandoned when during the World War Dr. Hamilton found it necessary to leave California.

Between 1920 and 1924 the Pasteur Institute developed plans for the establishment and use of an African anthropoid station in supplementation of its resources for medical research. The first published descriptions of the project are those of Calmette (20, 21), Director of the Pasteur Institute. It appears that in 1924 a station had been located at Kindia in French Guinea (Africa), ample grounds developed, and several buildings erected. Various medical inquiries have been in progress at Kindia since that date.

Beginning early in the century, Señora Rosalia Abreu gathered as pets on her beautiful estate in Havana a collection of monkeys and apes. Despite its relatively long existence this primate colony, recently utilized for studies in behavior by H. C. Bingham and Yerkes, and described by the latter in a semi-popular book (80), has only incidentally and to a disappointingly slight extent contributed to the solution of biological problems. At the date of writing, the Abreu colony is larger and more varied than ever in its history. Probably it is the most extensive and otherwise valuable collection of primates in existence.

On the assumption that a primate breeding station should be located in a tropical or subtropical climate and should be constituted the field and supply station of a well equipped, favorably located northern research institute or university, effort in America has been directed to the development of special provision for morphological, anthropological, physiological, sociological, and psychological study of the primates. With the organization of the Institute of Psychology at Yale University in 1924, arrangements were made for the use of anthropoid apes, and in the following year a special Primate Laboratory was established in New Haven. Thus far, chimpanzees only have been used in this laboratory. It has been



Courtesy of Mrs. Kohts

LADYGIN-KOHTS STUDYING VISUAL DISCRIMINATION IN THE CHIMPANZEE

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found possible to keep them in good condition and to work satisfactorily with them. The logical development of this plan, which is an outgrowth of Yerkes' pre-war efforts to achieve adequate provision for the thorough and inclusive study of the anthropoid apes, involves such institutional and departmental coöperation of biologists as will assure the efficient utilization of anthropoid materials and the early establishment of a subtropical breeding and observation station.

For two or three years during the World War, Madam Ladygin-Kohts, Director of the Zoö-psychological Laboratory of the Darwinian Museum, Moscow, kept in her institution a young chimpanzee which she used for experimental studies of sensory discrimination and perception. It is not indicated in her publications (48, 49) that permanent provision has been made in Moscow for the maintenance or study of apes.

The representations of Carl Akeley (3, p. 248) interested the Belgian Government in the establishment of a large national park in the Belgian Congo to provide safe habitat for several African animals which are in danger of extermination. In the midst of this great reservation is a sanctuary for the mountain gorilla (*G. beringei*). It is proposed to build in this gorilla preserve quarters for scientific observers.

On the whole, the spread and intensification of interest in the anthropoids, and in the meagerness of our knowledge, are vastly more encouraging than the measure of progress in the last decade toward provision for wise utilization of these relatively rare and strategically important materials of biology.

GENERAL AND HISTORICAL ACCOUNTS OF ANTHROPOID BEHAVIOR

Excellent general accounts of the anthropoid apes and of the history of our knowledge of them are few, within the period of this digest, and exclusively German. By far the best semi-popular and authoritative book is the thirteenth volume of the fourth edition of Brehm's "Tierleben" (16). In this, the latest, edition of Brehm's great work, four volumes are devoted to the mammalia and of these the last volume includes the apes. The work is remarkable for readability, scope and reliability of information, and abundance and excellence of illustrations.

Under the editorship of Carl W. Neumann, a large part of the description of apes originally presented in the "Tierleben" has been reprinted in a pocket-sized volume (17). The editor has extended the work by drawing upon recent experimental studies of anthropoid behavior. This handy volume constitutes an almost ideally concise and convenient source of general information about the manlike apes for those who desire introductory acquaintance rather than the detailed descriptions to be found in original sources.

Knauer (39), in a small volume which is decidedly less satisfactory in its illustrative materials, less convincing in its descriptions, and more popular than Brehm, has given a brief, readable account of the history of our knowledge of the apes, of their distribution, habits, and mental traits. An unusual feature of this work is its description of several widely known performing apes.

An article by Mahoudeau (53), chiefly historical, presents evidence for the conclusion that the African ape called gorilla by Hanno, the Carthaginian, was really a species of chimpanzee.

Aside from taxonomic works, which only incidentally and incompletely describe anthropoid behavior, no notable general contributions to this subject have appeared in English during the period of

this digest. Elliot's "Review of the Primates" (28) is an informational mine, but neither its psycho-biological descriptive materials nor its references suffice to carry the student far toward knowledge of behavior. The lack of a complete and reliable historical account of anthropoid behavior is an increasingly serious inconvenience to biologists. We therefore have assembled the materials and undertaken the composition of such a work. Somewhat to our surprise, hundreds of relatively inaccessible but more or less valuable sources contributory to knowledge of the natural history and psychobiology of the apes have been discovered.

CONTRIBUTIONS TO ANTHROPOID NATURAL HISTORY

Travelers, hunters, and naturalists continue to provide fragments of information on the manner of life of the apes. In the period of review there has been no single major contribution, although there are several which are distinctly worthy of note as containing some new observations or verification of previously recorded facts. Then, too, the apes have found their way into somewhat polite literature (Kearton, 37) and it is becoming increasingly difficult to distinguish between natural history and story.

What promised to be an exceptionally valuable contribution to the natural history of captive anthropoids and other primates was presaged by Pfungst (57) when in 1912 at the Berlin Congress for Experimental Psychology he presented a summary account of his studies of the behavior of some two hundred species of Old and New World primates in various German zoölogical gardens. So far as we have been able to discover, full report of his work has not been published.

Although Garner, long a prominent field observer of the African anthropoids, published several minor and popular articles between 1912 and his death in 1920, except for an account of the habits of the gorilla (30), they offer only materials previously published in his books. In connection with his hobby, the study of speech in infrahuman primates, Garner over half a lifetime intelligently and perseveringly studied the habits and life-history of the chimpanzee and gorilla. Because of his lack of scientific training and background and some serious inaccuracies of description, his books have been unfavorably criticised by biologists and their value has probably been underestimated.

There are few special contributions to the social relations of the manlike apes. Descamps (26) has offered a general discussion and Reichenow (59, 60, 61) has contributed valuably to the social psychology of the gorilla. From his experience as collector, Aschemeier (6) contrasts the behavior of the African great apes when attacked by man.

Among books which might be classified under travel, natural history, or story, because they partake of the qualities of each and are rapidly spreading knowledge of certain of the apes, are those of Akeley (1, 2, 3), Barns (8, 9), Bradley (15), Kearton (37), and Prince Wilhelm of Sweden (77). It is impossible to review these books adequately in this digest, but in later sections special mention will be made of their peculiar values as contributions to our knowledge.

Nests and nest construction in the apes have attracted a disproportionate amount of attention, but as a satisfying result information is now reasonably detailed and trustworthy. Certain, if not all, species and varieties of the three manlike apes build nests: the orang-utan and chimpanzee in trees, the gorilla sometimes in trees and sometimes on the ground.

The gibbon hides among leafy branches as do the monkeys. It is well established also that the orang-utan is primarily a tree-dweller, the gorilla primarily terrestrial, and the chimpanzee intermediate. From these types of ape the gibbon differs so extremely that it richly deserves separate consideration. Like the orang-utan, it is arboreal, but it is far more nimble and graceful in its movements.

Jennison (36), Burrell (19), and Yerkes and Learned (81) describe nest-building activities in captive chimpanzees, while Christy (23) briefly and critically comments on the work of Jennison. Reichenow (59), Aschemeier (7), and Barns (8) offer valuable contributions to our information about nesting habits in both the chimpanzee and gorilla. By Sokolowsky (70) the facts about anthropoid nest construction are systematically and comparatively considered. Although somewhat prolix his paper is the best single source of information.

The nature of most publications on anthropoid behavior suggests as basis of classification the type of animal studied. We shall therefore indicate, in brief paragraphs, the principal naturalistic contributions to our knowledge of the four types of ape.

Gibbon. Although he was interested chiefly in experimental study of vocalization and speech, Boutan (13, 14), in a gibbon which he kept for several years, was able to observe various forms of adaptive behavior. Unfortunately his reports give scant information aside from his experimental findings. A paper by Mahoudeau (51), although it contains no original observations, is useful as a summary, critical evaluation, and discussion of the work of others. It is mentioned here chiefly because the literature on the natural history of the gibbon is extremely meager. Shelford (67a) and Debeaupuis (25) offer interesting descriptions with certain fragments of new material, and in an unpublished manuscript, "The tree-walkers of the tropics," Mrs. Edith Taussig Spaeth reports the field and laboratory observations of Dr. Reynold A. Spaeth, whose promising program of work with the gibbons of Siam was cut short by his tragic death.

Orang-utan. Strangely few are the recent naturalistic studies of the orang-utan. There is a valuable paper by Kerbert (38) which deals chiefly with habits and life-history, and Shelford (67a) briefly considers general mode of life. Wallace's "Malay Archipelago" (76), the first edition of which appeared in 1869, we feel justified in mentioning here because the seventeenth edition or reprint appeared in 1922, but still more because during nearly sixty years it has stood as the best naturalistic description of the orang-utan.

Chimpanzee. In the period of this digest most naturalistic studies of the chimpanzee have been incidental to experimental inquiries and have therefore been carried on with captive animals. The following publications refine, if they do not greatly extend, our information about the habitat and the behavior of this, the most intimately known of the apes.

Comparisons of the chimpanzee with the gorilla, with respect chiefly to temperament, emotional expressions, and nesting habits, are offered by Aschemeier (6, 7) on the basis of his own observations. The animal trainer and showman, Sheak (65, 66, 67), contributes from his experience with the chimpanzee to our information about individual differences and docility in the most dramatic of the anthropoids. Noteworthy also are the

studies of life-history in the chimpanzee made by Montané (54) and von Allesch (4, 5).

Kohts (48, 49), Köhler (40–47) and Yerkes (80, 81), in connection with experimental studies of the chimpanzee, have had unique opportunity to observe daily life, individuality, disposition, and life-history. In their various publications they have presented materials which importantly supplement naturalistic descriptions.

It is not difficult to understand why during recent years the chimpanzee among anthropoid apes has monopolized the attention of experimentalists and the gorilla that of naturalists. The chimpanzee is relatively available, hardy, and coöperative in experimental work; the gorilla, by contrast, is relatively difficult to obtain, hard to accustom to confinement and to experiment with. Naturalistically speaking, the chimpanzee is well known, whereas the gorilla is imperfectly known and little understood.

Gorilla. The strictly naturalistic contributions to gorilla lore are both numerous and important. One of Garner's last reported professional undertakings was the capture of two young gorillas for the New York Zoölogical Park, one of which he finally succeeded in delivering to that institution in good condition. The event is notable because it was the result of a carefully thought out plan to capture specimens in Africa and there partially to domesticate them, accustom them to eat a variety of strange foods, and in general to prepare them for life in an American zoölogical park. Garner's experiences in taming and training the little gorillas, and his observations on diet, temperament, play and emotional expressions, have been simply and briefly recorded (30). A continuation of the story of the young gorilla brought by Garner to New York has been supplied by Hornaday (34), who, in addition to tracing the short history of the animal's life in America, contributes interesting general observations from his experience with other gorillas.

Reichenow (59, 60, 61) gives, by all odds, the most circumstantial and detailed description of the characteristics of the new-born gorilla and of the feeding and nesting habits of this ape. His observations bear more or less relation also to the development and condition of the senses and the appearance of various habits. In addition to rendering more certain our knowledge of gorilla nests and nest building, Aschemeier's papers (6, 7) report differences in temperament between the gorilla and chimpanzee and offer the opinion that the gorilla is not the less intelligent.

A healthy specimen of young gorilla during the World War came into the possession of Miss Alyse Cunningham of London, whose almost unique experience it was to keep the creature in good physical condition and contented until he became too large and difficult to manage in the household. Miss Cunningham's description (24) of John Daniel is of first-rate interest and practical importance. It is significant that this perfectly healthy young gorilla died within a few months after falling into the hands of the management of an American circus. The interest which Miss Cunningham's pet and her success with him stirred is evidenced in a measure by publications of Sir Ray Lankester (50) and Hornaday (35). Although she has published no additional reports, the writers happen to know that since the death of John Daniel she has kept for varying periods two other specimens of West Coast gorilla. Of these the first died from a head injury received in capture, and

the second, at last accounts, was in good health after some three years of life in captivity.

Reminding the reader of the days and exploits of Du Chaillu are the books of the collector-naturalist Barns (8, 9) whose knowledge of the mountain gorilla of the Belgian Congo is exceptional. His books contain the best available descriptions of the daily life of this rare anthropoid and of the history of our knowledge of it. Yet in this case even the "best" is extremely meager and unsatisfactory.

Almost simultaneously with the publications of Barns appeared accounts by Prince Wilhelm of Sweden (77) and Count Gyldenstolpe (31) of their expedition into the Lake Kivu region of the Belgian Congo in pursuit of gorillas. Hunting and killing is so conspicuous in their narratives that even though the information about the gorilla may be trustworthy, it is not likely to command the approval and confidence of the humane naturalist and conservationist.

Subsequent to the departure of the Prince of Sweden, but while Barns was still in the gorilla mountains, Akeley, representing the American Museum of Natural History in New York, conducted a small party thither with intent to secure a few specimens of the mountain gorilla for a habitat group in his Museum. The expedition has been delightfully described by one of its members, Mrs. Mary Hastings Bradley (15), who reports experiences in hunting gorillas. Akeley, in addition to several articles whose materials are largely second-hand, has published in his book "In Brightest Africa" (3) original observations and experiences in hunting *Gorilla beringei*.

Finally, the experiences of Benjamin Burbridge, hunter and nature lover, who has spent weeks in the country of the mountain gorilla hunting, observing, photographing, and capturing live specimens, have been partially recorded by him (18a) and by Sparks (73). From conversation with Mr. Burbridge we have discovered that he knows a great deal about the characteristics and life habits of the mountain gorilla which thus far he has neglected to record. He is distinguished also by having secured excellent motion pictures of mountain gorillas in the wild, and not less so by having taken alive eight specimens of the young of the species!

LIFE-HISTORY AND GENETIC RELATIONS

Few indeed are the significant contributions to the life-history and genetic relations of the anthropoid apes. In the period of digest the first paper to be noted is that of Montané (54, 55) who from the Abreu primate colony in Havana obtained data on the sex behavior and breeding of chimpanzees. He was the first to report the birth and early behavior of Anumá, the only chimpanzee known to have been born and reared in the Western Hemisphere. Most of the data presented by Montané still lack confirmation.

Blair (12) from the New York Zoölogical Park, and von Allesch (4, 5) from the Berlin Zoölogical Garden, report on chimpanzee pregnancies and the birth of young. In New York the young survived birth for only a short time, whereas in Berlin von Allesch had opportunity to study the behavior of mother and young over a period of weeks. In his general account of the Abreu primate colony and of our knowledge of affective behavior in the anthropoid apes, Yerkes (80) has devoted to the life-history of the anthropoids a chapter in which are assembled available facts concerning the period of gestation, infancy, and parental relations.

From these several contributions it

appears that the period of gestation in the chimpanzee is not less than seven, nor more than nine, months, that the new-born animal is practically helpless, and without parental attention and assistance perishes within a few hours. During the first few months of postnatal existence it is wholly dependent on the mother for nourishment, protection, and bodily care. Gradually it achieves independence through acquisition of ability to walk, in which it is assisted by parental tuition and is thus enabled to amuse itself in increasing measure, to seek food, and to develop steadily through play with others of its kind.

Publications of Reichenow (61) and Garner (30) are contributory rather to our knowledge of behavior in the young of the gorilla than to generation or parental relations.

STRENGTH, ENDURANCE, HEALTH

There is widespread conviction that the great apes are very strong, but until recently no measurements had been reported. In two papers by Bauman (10, 11) dynamometric measurements of the strength of the chimpanzee and orang-utan in comparison with that of man are offered. The procedure was far from satisfactory and the data are indicative merely of the order of strength. Whereas the maximum pull for an adult female chimpanzee was 1260 pounds, both arms being used, that for the average college man is 332 pounds. The author states that the chimpanzee's superiority to man on the basis of weight is in the ratio of three to one.

Unpublished observations by Yerkes indicate that the young mountain gorilla is, relative to weight, much stronger than man. These observations on strength suggest the important physiological question: By virtue of what circumstances of life or structural peculiarities are the muscular or the neuro-muscular mechanisms of the orang-utan, chimpanzee, and gorilla so far superior in working power to those of man, or is the seeming superiority to be accounted for by relative use?

Evidences of fatigue in the apes, especially in experimental situations which require novel adaptations of behavior, have been noted by various observers but never described with useful detail and exactitude. Boutan (13, 14) states that mental work rapidly fatigues the gibbon and induces yawning and finally sleep, and Yerkes has made similar observations on the chimpanzee and other primates.

Anthropoid diseases, health, and hygiene have not been systematically and adequately discussed by any single authority. The special chapters devoted by Yerkes (80) to this subject are perhaps as useful practically as anything available. He has dealt especially with environmental requirements of captive apes, covering nutritional, hygienic, and social factors. There are, to be sure, many references to diseases characteristic of the apes, and papers descriptive of pathogenic organisms which are commonly or rarely discovered in them. We have considered it inappropriate to include literature on parasitology or medicine in this digest.

From the various reports available to us and certain unpublished observations, we gather that the anthropoid apes in general are susceptible to many of the diseases of man and suffer peculiarly from them because of lack of protective immunity and ordinarily good physical condition and care. Mortality, we suspect, may be due more largely to the unfavorable conditions of captivity than to greater susceptibility to disease or even to lack of immunity. Our scanty knowledge

points to the conclusion that captive apes demand intelligent, scientifically based nutritional, hygienic, and social provisions, including shelter from the direct sun and from unusual cold or wet. There is nothing to prove that they are less adaptable than man or less capable of normal life and reproduction under varied climatic and social conditions.

PSYCHO-BIOLOGY OF SENSORY AND PERCEPTUAL PHENOMENA

Apart from naturalistic observations of sensory equipment and perceptual activity, there are few contributions to the psychophysiology of the senses in apes. Many authors intimate that their special senses are similar to those of man, but the evidence is scientifically inadequate. Indeed even the best of the experimental inquiries are technically weak and must be considered exploratory rather than conclusive.

The existence of highly developed senses of sight, hearing, taste, touch, and smell is amply attested by numerous naturalistic observers, among whom mention may be made of Barns (8, 9), Descamps (26), Debeaupuis (25), and Kearton (37). Furness (29) claims to have demonstrated color discrimination in the chimpanzee and orang-utan, using painted blocks. With the aid of a form-board he studied also visual discrimination of form. Attempts to teach his subjects to reproduce simple drawings and to tie knots, demanding unusual visual-motor connections, yielded few positive results.

The most extensive study of the psychobiology of vision in an ape is that of Kohts (48, 49). This investigator experimented with a young chimpanzee in an attempt to measure his ability to detect and react appropriately to color, brightness, form, size, and number. Complete account has thus far been published only of her study of color and brightness discrimination. The work was carried on in Moscow during the World War and it was impossible for Mrs. Kohts to command adequate technical resources. She therefore made use of the best available colored and neutral papers and painted objects.

The method employed by Kohts is novel, although not wholly new, and her use of it establishes its value for exploratory and qualitative work, if not for rigidly controlled and precise measurement. She calls it the method of "choice from sample." The animal was trained to sit at a table opposite the experimenter. On the table was placed an assemblage of objects to which the animal was taught to react by selecting and manually presenting to the experimenter one which in a given quality matched an object previously displayed by the experimenter as sample. Clearly the presentation of the sample object is equivalent to a command to match it from the objects available on the table. It is necessary then for the animal to search visually or otherwise for the appropriate object and on recognition to hand it to the experimenter.

Kohts, keenly aware of several possible sources of error, effectively checked her results in various ways. The visual stimuli which she necessarily depended upon are not readily describable with scientific accuracy, nor can they be duplicated easily by other investigators. There is also a possibility that the chimpanzee may have obtained certain assistance in the form of sensory cues unconsciously given by the experimenter.

The observations of Kohts, as summarized in her voluminous report, prove the ability of the chimpanzee to react specifically to wave-length (color or hue) versus intensity (brightness). Also that chromatic stimuli, closely similar in hue but differing markedly in satura-

tion, are more readily distinguished than are those which differ markedly in brightness but are very similar in saturation. The investigator believes she has demonstrated that the chimpanzee naturally depends rather on hue than on brightness in its response to colored objects. The degree of acuity in wave-length (color) versus intensity discrimination it was impossible to measure satisfactorily because of the nature of the experimental materials.

Worthy of note because of its unexpectedness is Kohts' conclusion that achromatic visual stimuli, with the possible exception of white and black, are not as readily distinguished by the chimpanzee as are chromatic stimuli.

Her investigation demonstrates with reasonable certainty the existence of color sense in the chimpanzee, but it fails to provide such detailed and reasonably accurate measurements of the value of different aspects or factors in visual stimulation as are desirable and essential for comparison of the visual equipment of the chimpanzee with that of man and other animals.

The experiments on visual discrimination of form, size, and number carried on by Kohts with the chimpanzee Ioni are only summarily described in her available publications. We are informed detailed report is in course of publication. With respect to these aspects of vision the investigator states that by the method of choice from sample she was able in a surprisingly short time to make a very large number of experiments which, in addition to the results above referred to, demonstrated ability to recognize and discriminate various planimetric and stereometric figures, objects differing in volume or in one of their three dimensions, and such objects as letters and pictures.

In brief, Kohts believes that she has proved that the visual equipment of the chimpanzee is, in its essentials, similar to that of man. As measurements of acuity were not made, it is impossible to go beyond this qualitative statement.

The experimental investigation of Kohts is the first detailed, systematic, reasonably thorough-going and highly illuminating investigation of the sensory life of an anthropoid ape. Whatever its technical shortcomings may be, its results are valuable as indication of the outstanding characteristics of chimpanzee vision and as basis for the formulation of specific problems in the study of this sense.

At the Canary Island Anthropoid Station Köhler (40, 41), working with chimpanzees, concentrated his attention on problems of perception, memory, and imagination, and more or less incidentally discovered sensory characteristics. Taking his cues from the characteristics of human vision and his problems from the classical literature of the psycho-physiology of visual perception, Köhler planned and carried out certain extraordinarily illuminating investigations. His work was done in the main under unusually trying conditions.

Response to achromatic stimuli, supplied by a standard series of neutral papers ranging from intense white to dead black, demonstrated, in agreement with the observations of Kohts, the ability of the chimpanzee to discriminate on the basis of small differences in brightness. Experimental procedure, although crude perforce of circumstances, was ingeniously checked and there can be little doubt of the reliability of the findings, although as in the case of those of Kohts, the statements of result are primarily qualitative.

Köhler presented, as stimulus objects, two adjacent boxes, the visual appear-

ance of which could be readily altered. The animal, by reaching for the desired box with a stick and drawing it to the netting through which the hand could be reached, secured as reward for correct choice a bit of some desired food. The box designated as the wrong one contained no food. Punishment for incorrect choices was not employed and the investigator doubts its efficacy with the chimpanzee.

Somewhat similarly, Köhler investigated the chimpanzee's ability to discriminate chromatic stimuli and to his satisfaction demonstrated, through positive results with red, blue, and mixtures thereof, the existence of color sense. In this case the materials were painted surfaces prepared at the station by Köhler and impossible of exact description with his facilities. The stimuli were presented behind circular openings ten centimeters in diameter in two like adjacent boxes. Color wheels, rotated to give complete fusion for human observers, were employed to produce the stimuli intermediate between the terminal blue and the terminal red. On its part, the animal was required to point either with arm or stick to the box which it selected as correct. Thereupon a food container was delivered to it by the experimenter. In case of correct choice this container supplied a reward; otherwise it was empty.

By comparison with his other contributions to the psychobiology of the chimpanzee, Köhler's studies of color and brightness vision are of minor importance. Yet because of the meagerness of our information the work commands critical and appreciative consideration.

With Kohts, Köhler agrees in concluding that discrimination on the basis of color is easier to the chimpanzee than similar discrimination on the basis of achromatic stimuli.

Only incidentally do the visual investigations of Kohts and Köhler contribute to our knowledge of the other senses in the chimpanzee. Hearing is relied on constantly as a guiding sense, but there is no convincing evidence that the animals use smell to supplement visual discrimination and choice. Both smell and taste, however, are regularly employed in testing objects which the animal suspects of being edible.

In the realm of visual perception the contributions of Köhler are epoch-making and undoubtedly will have a profound influence on the development of comparative psychology. Working with extremely meager instrumental equipment and resources, he displayed ingenuity and skill which should stimulate and inspire those who labor in poorly equipped laboratories.

Monocular vision was tested by placing the reward, a banana, at variable distances behind a wire screen before which the animal stood. To the animal in this position the experimenter handed two sticks, the one capable of being fitted into the other, so that the united pieces might be used to fish through the screen for the food. The subject was required to fit the pieces together: (1) with binocular vision; (2) with monocular vision; and the time required for the process was recorded as a measure of the value of visual function. The chimpanzee Sultan, a right-handed animal, yielded the following results: Time for binocular vision, 2.1 seconds; for monocular vision, right eye, 3.4 seconds; for monocular vision, left eye, 5 seconds.

In tests of visual perception of depth, it was demonstrated by an ideally simple procedure that a desired object could be correctly located in 84 per cent of choices with binocular vision; in 53.3 per cent with monocular vision, and in the case of a right-handed chimpanzee 58.3 per cent

with the right eye alone, and 48.7 per cent with the left eye alone.

In this experiment the chimpanzee was allowed to stand before a screen in which a small hole at the level of the eye permitted it to see a grape which was suspended on an invisible thread in the midst of a chamber. It was necessary for the animal visually to locate the grape as dropping either before or behind a screen which divided the stimulus chamber into two compartments. The subject in seeking its reward went, according to its perceptual data, either to the nearer or the farther division.

The question: Can an object be recognized by a chimpanzee as the larger of two familiar objects, even though its corresponding retinal image be the smaller? was affirmatively answered by the following experimental procedure.

On a table behind a wire screen, before which the animal worked, were placed two stimulus boards which constituted the visible fronts of food containers. The one board was much larger than the other. In the first instance the animal was trained to choose the larger box in order to get reward of food. Thereupon, the boxes were shifted in position so that the smaller was relatively nearer the screen and its image larger than that of the objectively larger board. Assuming that the animal is discriminating on the basis of visual size, this reversal in the relative size of the images of right and wrong boards should be followed by consistent choice of the objectively smaller stimulus area. The chimpanzee, however, continued to choose the larger board in spite of all changes in position, reacting thus as does man, and demonstrating presumably the existence of cortical or memory factors or contributions which either replace or supplement the immediately presented visual stimulus and constitute adequate basis for correct reaction.

Maintenance of the identity of visual objects amidst diversity of conditions Köhler demonstrated also in an experiment on the discrimination of widely differing neutral or achromatic stimuli. In this instance the one food container presented a white front to the animal and the other a black front. The animal was trained to choose the white as the correct reward-containing box. When this habit had been established, the experimenter suddenly altered the relative luminosity of the two stimulus surfaces by permitting direct sunlight to fall on the black surface. Thus it became relatively white and the other relatively black. The chimpanzee, nevertheless, continued to choose correctly, demonstrating the existence of other than the primary visual factor in its discrimination, and definitely raising the question of memory contribution.

Köhler's investigations occupied years and it is impossible within the limits of this digest to do more than characterize his methods and results in the study of sensation and perception and to exhibit them by samples. Even more significant in essential respects than his notable contributions of fact are his critical discussions of the historical methods of investigating sensory discrimination and acuity in infrahuman organisms and his suggestion of other experimental procedures.

STUDIES OF ADAPTIVE BEHAVIOR

Adaptive behavior, as here used, includes all conditioning of action from the modification of simple reflexes to the development of complex habit-systems which may involve ideation and purpose. The lay term 'intelligence' is generally applicable, but it is scarcely inclusive enough and its degree of applicability varies widely.

Observations relative to adaptive behavior in the anthropoid apes appear in a large proportion of the naturalistic

publications, and the writings of animal trainers are dominated by facts and reflections concerning the exceptional intelligence of the chimpanzee or other anthropoid. Peculiar, however, to the period of this digest is the appearance of several major experimental contributions to the subject. Without intending to disparage naturalistic work, or indeed the utilization of any opportunity to gain knowledge of anthropoid behavior, one may reasonably contend that definitely directed and controlled systematic and sustained study of various kinds or aspects of adaptive behavior in the apes is of preëminent importance and should rapidly refine, extend, and illuminate our knowledge.

To begin with certain relatively minor contributions—Haggerty (32), taking his cues from Hobhouse (33), by simple experimental procedure tested, in the New York Zoölogical Park, the ability of a chimpanzee and orang-utan to use a stick as a tool. Also he noted evidences of adaptive behavior in the daily life of his subjects. By his results, which were incidental to systematic experimental study of the imitative tendency in monkeys, he was led to believe that the orang-utan is superior in intelligence to the chimpanzee and that the behavior of both suggests perception of relations, a low order of rationality, and ability to profit by experience by something more closely akin to understanding of the situation than to the blind efforts of trial-and-error.

Acquaintance with the orang-utan having suggested to him its capability of indefinite profiting by educative treatment, Furness (29) undertook to acquaint himself intimately with examples of both the orang-utan and chimpanzee, and to train them by kindergarten methods to speak, read, and write. His experimental technique, although apparently adequate to his purpose, yielded little but negative results. In the course of the work he demonstrated various types of adaptation and became impressed with the ability of the animals to regulate their actions in accordance with sensory discriminations and perceptions essentially like our own.

In the end Furness concluded that his apes showed no "signs of reasoning." Yet in the same paragraph he states: "I am inclined to think, however, that such an act (unlocking door, turning spigot, etc., to get a drink of water) with the chimpanzee is governed by simple succession of ideas rather than by a prearranged sequence of actions, with a definite object in view." This statement enables one to evaluate the author's contribution to psychobiology.

Working also with orang-utans and chimpanzees, Shepherd (68, 69) in his application of simple experimental tests which he had previously used on monkeys, dogs, and cats, obtained results indicative of ideas, "probably of a crude and unanalyzed type." Shepherd and also Sheak (65, 66, 67), from observation of animals trained for the stage, have made observations pertinent to adaptive behavior. On this score Sheak's intimate acquaintance with performing animals entitles his statements of fact and his conclusions to serious consideration.

The first and only experimental study of adaptive behavior in the gibbon is that of Boutan (13, 14) who for five years carefully observed the daily life and adaptations of a female of the species, *H. leucogenys*. His initial interest was in vocalization, but he was presently led to undertake a comparative and experimental study of adaptive behavior in the gibbon and young child.

The methods of Boutan in this pioneer comparative work evidently were sug-

gested by the investigations of Thorndike and Kinnaman. They involved the use of problem boxes, each of which presented a relatively simple mechanism, by the proper manipulation of which food might be obtained from within the box. In some cases the mechanism was visible to the subject; in others, invisible. Boutan's observations bear the marks of critical care and his conclusions are of such considerable theoretical importance and have been so far ignored or neglected by psychobiologists that they are presented herewith in free abbreviated translation.

Boutan's principal conclusions (14, p. 142–43). (1) In these experiments the gibbon acquired by its own initiative new ideas. (2) It remembered the new ideas and the movements appropriate to the activity which led to their discovery. (3) The animal had prevision of the object to be attained, but not of the movements necessary. In its consciousness the idea of movement appears to be independent of the movement itself. (4) Under ordinary circumstances the animal manifests spontaneous or natural attention. (5) In exceptional cases one observes the beginnings of voluntary or artificial attention. (6) These flashes of the characteristically human sort of attention cause the animal great physical fatigue. (7) The young child *who has not learned to speak* works like the gibbon. Its performance seems even inferior to that of the ape; it opened the box with invisible mechanism as did the gibbon in the first period of work. (8) The child *who is beginning to talk* does not work like the ape. Instead its efforts are directed along a definite line. Its performance with the invisible mechanism is inferior to that of the ape and of the younger child. (9) The child who is beginning to speak works like a man; the child who does not speak works like an anthropoid. (10) The difference in method appears to be due not to difference in age but to conditions associated with the possession or lack of language.

With the definite intention of studying in contrast the method of solution of standardized problems by monkey and ape, Yerkes (78) for a number of months experimented with a young orang-utan. He used an original method known in the literature as the multiple-choice method, and supplemented his results by employing also a variety of simple problem tests, such as are commonly used by lay observers, by animal trainers or by psychologists whose curiosity impels them to do something with anthropoid apes.

By the multiple-choice method the investigator is enabled to present to any type or condition of vertebrate whose adaptive behavior he may wish to study, one or all of a series of problems ranging from simple to complex. All the problems are perfectly and quickly soluble by an organism which is capable of perceiving certain essential relations and of acting as does man when he experiences insight or the understanding of a significant relationship.

In this carefully planned type of experimental situation the behavior of the young orang-utan in some respects closely resembled that of man. Yerkes has cited the following as evidences of ideation: (1) Trial by the animal of several different methods in connection with each problem; (2) sudden transition from one method to another; (3) the final and perfect solution of a problem without diminution of initial errors; (4) the dissociation of the act of turning in a circle from that of standing in front of a particular box. Further, this investigator states: "The survey of my experimental records and supplementary notes forces me to conclude that as contrasted with the monkeys and

other mammals, the orang-utan is capable of expressing free ideas in considerable number, and of using them in ways highly indicative of thought processes, possibly even of the rational order. But contrasted with that of man, the ideational life of the orang-utan seems poverty-stricken. Certainly in this respect Julius [an orang-utan] was not above the level of the normal three-year-old child" (78, p. 132).

Although in her intensive study of the young chimpanzee Kohts was concerned chiefly with characteristics of vision, she incidentally observed many and varied evidences of adaptation of behavior, and in a few cases especially modified her experimental procedure to exhibit whatever types of adaptation the subject might be capable of. Thus, for example, instead of leaving the sample object which was to be matched by the animal in sight during the matching activity, she would display it for a few seconds, remove it from view, and delay the chimpanzee's reaction for a definite period in order to measure his ability to respond correctly under such conditions. It was found that correct choice continued up to approximately fifteen seconds delay, but beyond twenty seconds the ape usually responded incorrectly.

Experiments of Kohts, in which the ape was required to select the correct object by some one quality, as for example color, from among a group of objects differing in form, size, and color, indicate, she believes, certain limited power of abstraction. The presence of ideas is inferred from the characteristics of the animal's adaptive behavior, and it is stated that the practical conclusions arrived at by the animal seem to be based on something akin to thought processes.

In general the evidences of ideational behavior in this anthropoid reported by Kohts, and her conclusions, are similar to those of the more thoughtful and critical of naturalistic observers, animal trainers, and psychologists who have applied certain simple tests of intelligence.

Köhler, during his prolonged period of service at the Canary Island Anthropoid Station, devoted a large portion of his time to experimental analysis of adaptive behavior in the chimpanzee. Fortunately, he had several healthy immature animals and was able to compare individual differences and, in a measure at least, to escape the undesirable human influence which to an indefinite extent vitiates work with animals trained for the stage. Throughout his prolonged investigation he apparently kept in mind the question: Does the chimpanzee act with insight under conditions which require it?

In securing evidence of the ability of his animals to solve novel problems and in gaining accurate knowledge of their methods of solution, Köhler used not only the types of simple test procedure previously suggested or used by Romanes, Hobhouse (33), and others, but added many ingenious and appropriate situations of his own invention. He did not, however, despite abundant and excellent opportunity, use the method of insoluble problems devised by Hamilton (Jour. An. Beh., 1, 33), the delayed reaction method of Hunter (Beh. Monos., serial no. 6), or the multiple-choice method of Yerkes (Jour. An. Beh., 7, 11).

According to Köhler's classification (41), he depended upon four principal types of problem method, designated by him as round-about methods, the use of implements, the making of implements, and detours around separate intervening objects. In each case, the essential feature of the situation is the possibility of securing reward by the performance of an act which depends upon the perception of

some important relationship. For example, a banana, lying outside the cage and beyond arm's reach, may be obtained by using a stick which lies on the floor of the cage; or, in another experiment, by straightening a bent wire and using it to reach and pull with. Or, a food container may be brought within reach by going to a remote corner of the cage and unhooking a rope which supports the container. Food suspended from the ceiling of the cage may be reached by the stacking of available boxes or by the use of a ladder. Obstructions in some instances may have to be removed or so placed that they will serve a useful purpose.

The author's detailed descriptions of the behavior of his animals in the numerous and extremely varied problem-situations are illuminating beyond comparison with any previous work, and his results and conclusions are entirely consonant with those of other authorities who have studied experimentally the chimpanzee and orang-utan (see 32, 49, 69, 78, 80).

As his principal conclusion from the study of adaptive behavior, Köhler states that the chimpanzee exhibits intelligent behavior which in man is accepted as indicative of insight, understanding, and the functioning of ideas. He takes pains to point out that his observations are consistent with the prevalent conception of organic evolution and support the correlation of intelligence with brain structure. The lack of speech is singled out as one of the chimpanzee's chief disadvantages by comparison with man, and next to it the absence of our sort of visual space forms with appropriate relations to motor processes makes the human world a very confusing place for the ape.

This brief objective description of Köhler's contribution to anthropoid psycho-biology seems hopelessly inadequate. His work is in a sense epoch-making, because it displays ingenuity, adaptiveness, insight, constructive imagination, power of self-criticism as well as of the methods and conclusions of others.

The first experimental study of the gorilla, involving measurement of adaptivity and systematic observation of habits in captivity and of emotional expressions, was begun by Yerkes near the close of the period of this digest. The results, now in press,[1] although limited to a single specimen of the mountain gorilla, will afford a better basis for comparison of this rare ape with other types of primate than did previous naturalistic observation.

Yerkes and Learned (81), in a report which is chiefly devoted to vocal expressions and their significance in the chimpanzee, present evidences of adaptive behavior gained from observation of the daily life of their animals and from experimental studies directed to the exhibition of adaptivity and the demonstration of whatever ability the animals may have to work from insight.

TEMPERAMENT, DISPOSITION, AND EMOTIONAL EXPRESSIONS

Many of the naturalistic papers descriptive of the habits and environmental relations of the apes contribute fragmentarily to our knowledge of disposition and emotional expressions. The following references are worthy of mention: Aschemeier (6), Barns (8, 9), Boutan (13), Cunningham (24), Garner (30), Hornaday (35), Kearton (37), Lankester (50), Reichenow (61), Rothmann and Teuber (64), Sokolowsky (70), and Sparks (73).

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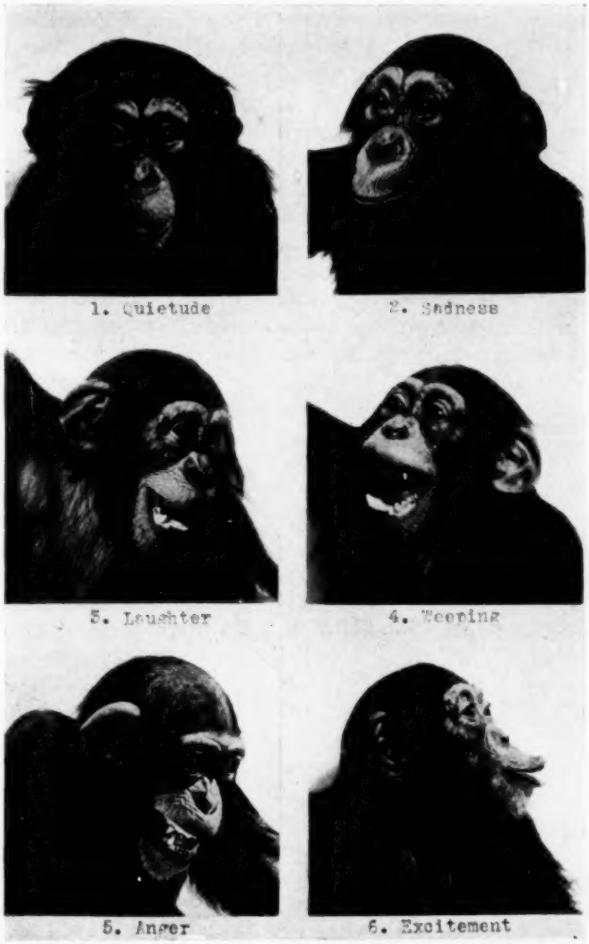
[1] Genetic Psychology Monographs.



Courtesy of Mrs. Kohts

EMOTIONAL EXPRESSIONS OF IONI, A FIVE-YEAR-OLD CHIMPANZEE OBSERVED BY MRS. LADYGIN-KOHTS IN MOSCOW

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chimpanzees Sheak (65) considers individuality and temperamental traits in captive specimens which he has known.

For the young orang-utan Yerkes (78) records temperamental characteristics and emotional expressions under ordinary conditions of life in captivity and in experimental situations as well. The affective characteristics of two young chimpanzees are described by Yerkes and Learned (81), and in a somewhat more general and systematic work Yerkes (80) gives an account of the emotional life of the chimpanzee and orang-utan, based on observations at the Abreu primate colony and on the data of the available literature.

Kohts (49) and Köhler (41, 44), working simultaneously with chimpanzees, have contributed important facts of affectivity. Their careful descriptions make clear the conspicuousness of individual differences and the similarity of the apes to man in temperamental constitution and in dominant emotional expressions. Kohts states as her opinion that the chimpanzee more closely resembles man in its affective than in its intellectual life. She obtained in connection with her experiments and has published (49) some splendid photographs of emotional expression in the chimpanzee.

VOCALIZATION, SPEECH, LANGUAGE

Garner, the outstanding specialist on speech in infrahuman primates, published nothing on this subject within the period of our digest. His notable books, which, like the famous DuChaillu description of the gorilla, have been unfavorably and perhaps also unfairly criticised by the scientific world, antedate this period. No one has seen fit to follow in Garner's footsteps by making the study of primate speech a hobby. The subject, however, has not been wholly neglected and there are several publications which deserve comment.

Following general observation of the vocalizations of the chimpanzee and orang-utan, Furness (29) attempted by various means to teach specimens of these apes to talk. By diligent effort he succeeded in getting them to pronounce two or three words. Although discouraged by their slow response to training, this observer concludes (1) that the orang-utan is more promising as a conversationalist than the chimpanzee because it is the more patient, less excitable, and takes more kindly to instruction; and (2) that in comprehension of the significance of words for objects and actions, the orang-utan and chimpanzee exceed domesticated animals. He states that both of his apes were able to understand what was said to them better than any professionally trained animals he had ever seen.

The vocalizations of the gibbon, often commented on by travelers because of their unusual quality, have been well described by Mahoudeau (52). With special interest in the origin of language and of the relation of vocalization in the other primates to speech in man, Boutan (13) for some years studied the vocal expressions of the gibbon. The title of his report "Pseudo-language" suggests his principal conclusion. He discovered that the animal is capable of varied vocalizations which may be classified as: (1) Expressions of satisfaction and well-being; (2) expressions of discomfort, illness, or fear; (3) expressions indicative of intermediate conditions, and (4) expressions of great excitement. He states that the characteristic sounds made by the wild gibbon are innate and not the result of parental education or imitation of the behavior of its fellows. He further is convinced by his observations that this ape does not use sounds in a verbal sense,

as symbols of objects or actions, but merely as expressive of emotions. Boutan's monograph on pseudo-language is at once the most interesting and the most valuable of the studies of vocal expression in this type of ape.

The most recent published account of chimpanzee vocalizations and effort to teach this ape to speak is that of Yerkes and Learned (81). The latter recorded in musical notation the various vocalizations of two young chimpanzees, seeking also to discover the significance of the sounds; and the former undertook by simple experimental procedures to train one of the animals to reproduce sounds in association with objects. The results of this instructional attempt were almost wholly negative and they convinced the investigator of the slight tendency in this ape to reproduce auditory stimuli or to imitate sounds produced by its kind or by man. This record of chimpanzee vocalization is uniquely valuable because of its relative completeness and its definite information as to the quality and natural uses of the voice in the young of the chimpanzee.

In a general chapter on anthropoid speech and its significance, Yerkes (80, p. 165) offers a résumé of notable contributions, and attempts to indicate definitely the present status of our knowledge. His discussion concludes with the statement: "Everything seems to indicate that their vocalizations do not constitute true language, in the sense in which Boutan uses the term. Apparently the sounds are primarily innate emotional expressions. This is surprising in view of the evidence that they have ideas, and may on occasion act with insight. We may not safely assume that they have nothing but feelings to express, or even that their word-like sounds always lack ideational meaning. Perhaps the chief reason for the ape's failure to develop speech is the absence of a tendency to imitate sounds. Seeing strongly stimulates to imitation; but hearing seems to have no such effect. I am inclined to conclude from the various evidences that the great apes have plenty to talk about, but no gift for the use of sounds to represent individual, as contrasted with racial, feelings or ideas. Perhaps they can be taught to use their fingers, somewhat as does the deaf and dumb person, and thus helped to acquire a simple, nonvocal, 'sign language.' "

SOCIAL RELATIONS AND INSTITUTIONS

Only one article devoted exclusively to sociological considerations has been found. It is that of Descamps (26) who briefly compares social phenomena in the anthropoid apes with those in primitive man. The principal categories of social phenomena used by this author are: means of existence, mode of existence, and group life. In each, marked similarities as well as differences among the types of anthropoid ape and between them and primitive man are noted. Although this author makes no contribution to our knowledge of social relations in the apes, his discussion convinces one of the great importance and promise of this field of inquiry and stirs interest.

From his sustained observation of immature chimpanzees Köhler contributes significantly to anthropoid sociology. He was able to observe the social behavior of young animals, both male and female, but had no opportunity to study parental or family relations. This is equally true of Yerkes (81) who noted various relations between his two young chimpanzees, and also the attitude of each toward other creatures in their environment. The contribution of Kohts, since she worked with a single ape, is limited to its behavior and relations to other types of organism.

Drawing his materials largely from the

chimpanzee group in the Abreu anthropoid colony, Yerkes (80) has been able to describe somewhat more fully and systematically the relations between apes of the same or different age, between the sexes, in the family group, and between father and offspring and mother and offspring. This account, although far from complete and doubtless wholly inadequate in many other respects, advances the subject by bringing together scattered observations and by supplementing it in the light of the occurrences in an extraordinarily interesting anthropoid colony.

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STUDIES IN THE GENERAL PHYSIOLOGY AND GENETICS OF BUTTERFLIES

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INTRODUCTION

THE exquisite colors of diurnal butterflies are such a source of pleasure to the collector that the amateur is often content with the classification and description of his dried specimens. But to one who has watched day by day the growth and transformations of many butterflies, such a collection in spite of its beauty seems like a gorgeous mausoleum. One misses the reactions of the graceful live creatures in response to sunlight and shadow, to the varying lure of different flowers, to their mates, to man and other giants which invade their field of vision.

Each live butterfly has its personality. It behaves, in the first place, according to the customs of its own family, genus and species, for the instincts of each clan differ strikingly as we shall see. It differs, moreover, from other representatives of its own species and even its own brothers and sisters, in vigor, longevity, fondness of the other sex and of its food, its response to light and shade.

Let us take for example the colony of caterpillars of *Vanessa antiopa* from the same mother, which I brought into the laboratory in June, 1924. They emerged as adults within two or three days of each other during the first week in July. A few caterpillars had died of wilt or *flacherie*, a boon to the farmer but a pest to the silk raiser and student of genetics, to which one male butterfly succumbed a few days after eclosion.

LONGEVITY

This group of butterflies was under observation in the greenhouse for six months,—the last survivor living until Christmas—in a cage 18 inches square, consisting of a frame covered with soft netting. A bunch of fresh flowers dipped two or three times a day in water sweetened with brown sugar to the consistency of maple sap was always within their reach at the top of the cage. Deaths occurred as follows:

	sex	age
September 6..............	female	2 months
November 10..............	female	4 months
November 10..............	female	4 months

Meanwhile out-of-doors fresh antiopas of the second or autumn generation had appeared. The little colony in the laboratory had outlived the usually recognized limits of its own generation. One was killed by accident; one escaped; the remainder lived until the following dates:

November 18.....	male	20 wks.	= 4½ mos.
November 20.....	female	20 wks.	= 4½ mos.
November 26.....	female	21 wks.	= 4¾ mos.
December 6.....	female	22 wks.	= 5 mos.
December 19..	2 females	24 wks.	= 5½ mos.
December 22.....	female		

The last survivor was still alive, though feeble, on December 24, aged 25 weeks,

or about 6 months. This is probably not unusual in this species and a few allied species which hibernate as adults. The autumn brood regularly hibernates, and Dolley (1916) also records that six individuals of *Antiopa* lived in his laboratory from August to the latter part of February, that is, for six months.

The normal life of an adult butterfly of *Colias philodice*, however, is much shorter than of *Vanessa antiopa*, an average of not over three weeks in summer; it is prolonged somewhat by cold conditions. Hibernation, however, very rarely occurs at this stage, and I have never succeeded in wintering the pupa. The young larva in the second or third stage regularly hibernates.

Seven sisters eclosing the last of June (in 1921) lived from 15 to 28 days with an average of 18½; three others in April–May lived an average of 20 days, which may be regarded as about the normal period. Three sisters eclosing the last of August (in 1920) lived, however, an average of 27⅔ days, ranging from 23 to 33. The record for longevity of a female in activity was six weeks (August 23–October 5) during the autumn.

The most interesting features of the behavior of this colony of *V. antiopa* were their extraordinary stereotropism, or "death-feigning" instinct, their gregariousness, or tendency to gather in clusters like the caterpillars of this species, and their geotropic posture while at rest (corresponding to the head-downward position of the pupa).

STEREOTROPISM

When a butterfly of the genus *Colias* with its wings closed over its back is carefully laid upon its side upon a flat horizontal surface, it will lie quietly, provided it is not overexcited and its feet are not stimulated by contact with something solid. This instinct is far more highly developed in *V. antiopa* than in *Colias philodice* and *C. eurytheme*. When picked up by the wings and placed sidewise upon a table or upon a bunch of flowers, *Antiopa* draws in its feet and lies in a passive, inert state. If the light and heat are not intense, it may be tossed about without response, like any "death-feigning" insect, and will lie for a long time on its side. Gentle pressure upon the under side of the closed wings produces this quieting effect; even lifting the butterfly by the costal margins of the closed wings is sufficient to make it draw up its legs against the body and come to rest. I have found also that certain moths which spread their wings horizontally when at rest, if carefully inverted so that the upper surfaces of the wings are under gentle pressure, will lie quietly upside down, provided their feet are not stimulated by contact with any solid object.

This instinct in its incipient stages can hardly be regarded as protective and useful. It is the very simple quieting effect upon the neuro-muscular system produced by gentle pressure upon the wing surfaces, an inhibitory reflex, resulting in rest.

GREGARIOUSNESS AND POSTURE AT NIGHT

Gregariousness in *Vanessa antiopa* appears in their strong tendency to creep together into close clusters in the corners of the cage, usually toward the source of light. Compact groups of individuals resting head downward are regularly found in the cage at night. *Colias* never does this; they are always well scattered at night over the flowers in the cage and upon its walls, showing a strong tendency to hang wings downward, but not, as a rule, head downward. The wings-downward position is the characteristic nocturnal habit in *Colias* in the fields. Rest-

ing in this way, the wings are well protected even from torrents of rain. I have not investigated the reason for gregariousness, which is quite a different thing from the positive phototropism common to all butterflies in flying in bright sunlight and which brings *Colias* together at the top of a cage under such conditions. It is perhaps an olfactory attraction, and may be the same tropism which, in *Antiopa*, holds together in a colony the caterpillars from a single laying of eggs.

GEOTROPISM IN ANTIOPA

The third striking characteristic of *Antiopa* is the head-downward position when at rest. Parker (1903) has described this as negative phototropism, the head, after the butterfly has alighted, being turned away from the source of light. The light in my greenhouse comes chiefly from one side, not vertically downwards, and yet *Antiopa* usually rests with its head pointed straight downward with the axis of the body vertical. The presumption is strong that gravity rather than light is a determining cause.

To test the phototropic factor, I covered the cage with black cloth and arranged a mirror so that illumination was exclusively from below. One entirely satisfactory test, with a mirror, tended to support the theory that light is effective in determining the posture, for I once found the individuals on the vertical walls, all resting head-up, turned directly or obliquely away from the source of light. This is in striking contrast with the head-downward position which is usually observed even when the top of the cage is covered with black cloth. The experiment should be repeated on a larger scale.

Observations on the antiopas as they grew older and feebler threw new light on the problem. Owing to the atrophy of their fore-legs (as in all Nymphalids) they have more and more difficulty as they become advanced in age in holding themselves head upward on a vertical surface; their center of gravity is too high, so they swing around into the much more stable head-downward position.

Owing to this peculiar head-downward posture, which is evidently connected with the *lack of functional fore legs*, *Antiopa* has become adapted *when at rest on tree trunks* to light rays striking it from above and behind. Accordingly, after alighting on the ground, as well as when resting on a tree trunk, it turns tail toward the source of light, as Parker observed, though it always tends to creep and to fly toward a moderately strong light. Thus the apparent paradox of a positively phototropic insect facing away from the source of light when at rest is more clearly understood. This butterfly is adapted to receiving light from behind, an adaptation which begins even in the chrysalis, for the butterflies which have been observed to turn the head away from the source of light upon alighting are Nymphalidae and, as chrysalids, are suspended head downward. It is probably too early to say that all Nymphalids behave in this fashion, but I have recently had the opportunity of observing in the bright sunlight of the Mediterranean coast two common Nymphalids, *Pararge egeria* and *Vanessa cardui*, which regularly turn away from the source of light upon alighting, lowering their wings to a horizontal position.

GEOTROPISM IN COLIAS

A striking peculiarity of *Colias philodice* and *C. eurytheme*, in which they differ from *Vanessa antiopa*, is their positive geotropism in darkness. When a cage full of *C. philodice* and *C. eurytheme* flying actively in sunlight and at a high tempera-

ture is carried into a dark room, their activity continues for a minute or two. They do not fly upward as Parker has observed *Antiopa* to do in a dark room, but violently downward, repeatedly striking the bottom of the cage. The noise produced as they hit the floor in their hopping flight reminds one of a popper full of snapping corn over a bed of hot coal.

An unconfined butterfly of this genus in a weak light no longer flies upward but downward. It jumps or flutters at random about the floor of the room, or upon the ground, and soon comes to rest. Females which have begun to lay actively, especially if also old and feeble, fly very close to the ground.

PHOTOTROPISM

Light and heat have the most powerful control over the activities of diurnal Lepidoptera. Increase in light and heat, up to a very high intensity, stimulates activity. Bringing a cageful from darkness into strong light does not, however, produce an immediate reaction. A period of adjustment of about a half minute in *Colias* is necessary before activity starts and the butterflies begin to hover at the top of the cage.

When attuned to daylight, as they are in the fields, sudden increase of light, due to the floating away of a cloud, produces an outburst of activity and, if internal physiological conditions concur, the butterflies soar far upward. An oncoming cloud, if it cuts off much light, will send every butterfly to cover, though individuals, and especially species, differ greatly in this respect.

TILTING POSTURE WHEN RESTING IN SUNLIGHT

If a cageful of *Colias philodice* is brought into the slanting rays of the morning or late afternoon light (about 45° above the horizon), those resting on the floor of the cage often tilt the body and folded wings away from the source of light. The rays strike at right angles the exposed surface of the wings. Resting butterflies remind one of the leaves of plants which slowly turn themselves into a similar position in respect to the sun's rays, so that the whole exposed surface is evenly illuminated (fig. A). If a tilting butterfly resting on the ground is picked up and turned around 180° on the same plane, so that it now faces in the opposite direction, it will again tilt away from the light, though this time the other side of the body and under surface of the wings of the other side are exposed to direct sunlight.

This adjustment is made by the flexure and extension of the legs, as described by Garrey (1918) in the robber fly, except that this fly leans toward, rather than away from, the source of light.

Previous writers have not taken account of a possible sensitiveness of the wings to radiant energy (heat rays probably). If we should assume that in both cases the insect tilts itself until the wing surface is evenly illuminated, the apparent contradiction between the two insects would disappear. The robber fly's wings are, of course, held horizontally over its back instead of vertically. Accordingly, it leans *toward* rays coming obliquely (45° above the horizon), while the butterfly with wings closed above its back when resting on the ground, leans *away* from the source of light. In both cases, the light waves strike the plane of the wings at right angles.

But this idea does not take into account the fact that the compound eye is certainly involved. A robber fly with the lower part of its eyes covered, stretches upward; with the upper part covered, it crouches upon the ground; it leans toward

light striking its eyes sidewise. Its body and eyes stretch toward the light. The butterfly, on the contrary, if resting on the ground, rolls over on its long axis, away from the light. This might be described as negative phototropism when at rest and the matter dismissed, but it is

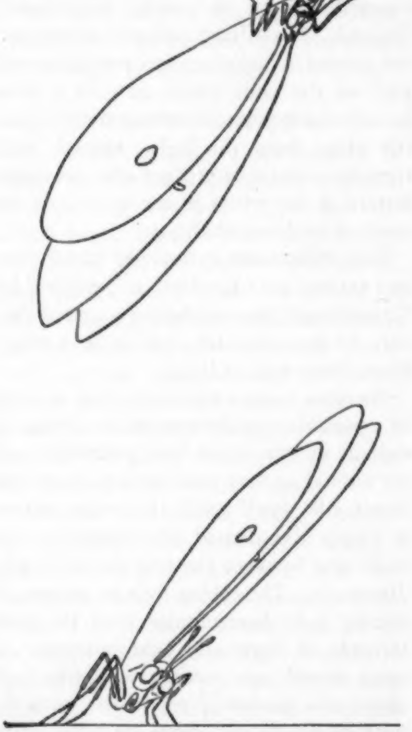


FIG. A. POSTURE OF BUTTERFLIES OF THE GENUS *Colias* IN RESPONSE TO DIRECT RAYS OF SUNLIGHT

not so simple as that, for I have often observed in a cage containing many butterflies (*Colias philodice* and *C. eurytheme*) and in which the light was coming through the netting obliquely from above, that those clinging to the top of the cage, with furled wings and back turned downward, tilt, like the robber fly, *toward* the source of light, while others resting on the bottom of the same cage are tilting *away from* the light (fig. A). In both positions the plane of the furled wings is perpendicular to the slanting rays of the sun; all parts are equally illuminated, like the leaf turned broadside to the light.

It is, of course, highly probable that the eyes are involved in this adjustment. One may imagine that the central facets, *i.e.*, ommatidia, may be more sensitive to light received from stationary objects and adapted for use when the butterfly is at rest, while the other parts of the eye are sensitive to light from moving objects which tend to disturb the repose of the insect. Possibly the latter are connected more directly with motor nerves, the former with nerves which inhibit muscular action. There is, however, the possibility that the wing surface itself is sensitive to light or heat waves, and that, just as the mourning-cloak butterfly rests with the upper surfaces of its expanded wings fully exposed to the direct rays and its head turned away, as Parker has described, so in *Colias* and other butterflies which close their wings we may have a reaction in which sensory impulses from the wings supplement those from the eyes. One certainly gets that impression in watching groups of listing butterflies resting on the moist ground out-of-doors on a summer morning.

Recently on the Riviera I had the opportunity of observing eleven individuals of the green hairstreak, *Callophrys rubi*, sprinkled over a lavender plant in full bloom, each with wings closed above its back and each listing at right angles to the sun's rays except when momentarily changing position during feeding. Thus certain Lycænidæ, like certain Pieridæ, list in the sunlight, unlike those Nymphalidæ which, upon alighting, turn away from the light and open their wings so

that the upper surface is exposed to the direct rays of sunlight.

FEEDING

A butterfly does not deliberately seek food. If the weather is cold and cloudy, it does not feed at all except that, when sufficiently stimulated by an increase in temperature or intensity of light, it extends its tongue to take moisture from the object on which it rests. The flying butterfly, controlled enormously by light rays, gets its food in a very casual fashion. The flower presents a bright reflecting surface on which it alights; then the moist, warm surface brings about the extension of the tongue and the rest of the feeding reflex. The moist surface of the hand or of the ground, certain flowers, like phlox and clover, are almost certain to make the tongue extend. Other flowers, particularly the geranium, have an inhibitory effect, or none at all.

Thus smell probably has a stimulating or inhibiting effect supplementary to light, in controlling feeding in the butterfly, whereas the nocturnal moth depends still more largely upon smell in finding and taking food, as it does in mating.

MATING

Mating in butterflies takes place in bright sunlight or at high temperature, but a sudden increase in intensity of light or heat sometimes brings it about in comparatively weak daylight and cool weather.

In the field, coupling often occurs during flight, and the male sometimes carries the female a considerable distance before alighting. Individuals ready to mate are unusually active. The female flutters with depressed wings and upturned abdomen. The male approaches from the side when the female is in flight or clinging to a plant or other object, presents his abdomen, and union suddenly occurs by the action of the male's clasps and hook. Then the female drops passively, and hangs attached to the male, facing in the opposite direction. The hind wings of the male overlap and half-conceal the hind wings of the female. He supports her weight in flying. When they are standing on a horizontal surface, he drags her about, while she loosens her foothold and allows herself to be pulled. If one holds the male by the costal margins of the forewings, the female remains passive, but if, on the contrary, the female is held, the male never hangs limp but swings round to get a foothold on one's finger or flutters violently.

Mating lasts usually about an hour, varying from about fifteen minutes to several hours. In my breeding experiments it has sometimes been necessary to pull members of a pair apart to prevent their remaining attached together indefinitely.

One coupling is sufficient for a female's whole lifetime. It rarely happens that a few infertile eggs are laid late in life. In the field a female may probably mate with several males successively, and any wild female may be confidently expected to be fertile. Mating occurs in *Colias* as soon after eclosion as the wings are dry. I have frequently brought about successive matings of a single male with three or four females.

EGG-LAYING

The flight of a female is always controlled largely by light, but as she grows older she gradually loses her strong instinct to fly upward and tends to settle upon the bright reflecting surfaces of the leaves to deposit her eggs. The touch of her feet upon the surface of a leaf and the odor of her special food plant causes the flexion of the abdomen. *Colias philodice* alights

on the sunward side of the potted clover plant with her back to the light, crawls to the summit of the leaf, bends her abdomen till it touches a flat surface and then deposits the egg. In *Colias* it is a spindle-shaped egg standing upon end, stuck to the leaf by the secretion of the cement gland acquired as it passes out of the oviduct. It is interesting to grasp an actively laying female by the front margins of the fore-wings and, with her coöperation, place eggs where you will on well-chosen leaves, distributing them with a view to providing plenty of clean food for the little caterpillars when the eggs are hatched. It is like using a rubberstamp, a delicate planting machine. In this way, the whole output of eggs may be increased and disease from overcrowding avoided. Crowding frequently occurs if a caged female is inactive and lays repeatedly on the same leaf. If active, she usually takes flight after each egg is laid, and so distributes the eggs somewhat widely.

ACTION OF LIGHT ON THE COLOR OF CHRYSALIDS

It is well known that Poulton in his "Colours of Animals" has described his extensive and interesting experiments showing that in *Vanessa urticæ* and *V. io* yellow and golden chrysalids are produced if the full-grown caterpillar, after it has stopped feeding, come to rest, and begun to spin its silken attachments, is placed in a yellow-lined box under a yellow screen; whereas caterpillars of the same brood, under blue rays, develop into dark colored chrysalids. Similarly in *Pieris brassicæ* and *P. rapæ*, yellow rays were found to favor the production of green pupæ, blue rays of dark gray pupæ marked with black spots. Other species are similarly responsive, e.g., *Vanessa atalanta*, like the other Vanessids, and *Papilio nireus* of Africa, which is particularly susceptible to changes in the quality of the light.

Poulton for convenience divided the period in the life of a full-grown caterpillar, after it has ceased to feed, into three stages: (1) *wandering*, (2) resting in one place preparatory to spinning its silken supports, (3) *fixed*. The period of susceptibility to the action of light was proved experimentally to be during stage (2) and the beginning of (3), that is, while resting preparatory to spinning and immediately after it.

Poulton entertained the idea suggested by Mendola (1893) that the light might produce its effects through the eyes, so he covered the ocelli of caterpillars of *Vanessa urticæ* with black varnish, but found that the pupæ were unaffected by the blindfolding, contrary, as we shall see, to the recent results of Brecher. The experiments of Fräulein Dr. Brecher on these two genera have been most thorough and have gone far toward a physico-chemical explanation of the phenomena.

Two pigments, green and black, are found in the chrysalis; the white color seen in the hypodermis and cuticle probably being a structural effect. The green, soluble in ether, alcohol and petroleum-ether, is called by Przibram and Brecher (1919) a lipochrome (fat-color), the term commonly applied to yellow carotinoid pigments associated with fats in animals. Its composition has not been determined. Whether it is identical with the apparently chlorophyl-derived green in *Colias*, which is not light-sensitive, is in my opinion doubtful. Przibram (1913) designates as "Tiergrün," a great variety of green animal pigments which, he holds, have no relation to chlorophyl, and it is extremely probable that some of them have not. In the Orthoptera, for

example, in which the blood is not green and some of which like *Carausus morosus* are said to develop their green coloration on an exclusively carnivorous diet, there is no reason to suppose that the green pigment is a slightly modified product of chlorophyl. Brecher (1917, 1921b) holds the same to be true of the green pigment in *Pieris*, regarding it as probably the product of the action of an enzyme.

The black pigment is known to be due to the action of an enzyme in the blood, designated as tyrosinase, upon tyrosin produced by the breaking down of proteins. Variations in melanic coloration depend upon the strength of the action of the enzyme. Thus Brecher (1917) found the tyrosinase in the blood of green pupæ less active than in that of the dark. The blood of whitish pupæ contains a tyrosinase which has the peculiarity of turning tyrosin red before becoming black, differing from the blood of all other color varieties, in which the reaction shows a preliminary violet.

The effect of light upon the tyrosinase was shown by experiments *in vitro*. The tyrosinase in blood drawn from caterpillars during the critical period and exposed for four days to yellow rays became less active; while on the contrary that exposed to ultra-violet rays became very active (1921a). The results of these experiments *in vitro*, however, are somewhat less convincing when we find that under other conditions (tyrosinase from agaricus and other periods of exposure) exactly opposite results were obtained (Przibram and Brecher, 1919); exposure of tyrosinase to yellow light increased its activity. In the *in vitro* experiments, moreover, the blood was first precipitated by ammonium sulphate and the precipitate dissolved in a n/80 NaOH solution. Untreated caterpillar blood normally turns black a few minutes after exposure to the air.

Brecher at first believed that the activity of the tyrosinase depended upon variations in its acidity, increased acidity destroying its efficiency. Yellow light accordingly was supposed to increase the acidity, ultra-violet to favor alkalinity. Her recent experiments (Brecher, 1925), however, carried on with great care by delicate methods, showed that the H-ion concentration of the blood of caterpillars and pupæ of *Pieris brassicæ* in different periods of life and when exposed to light rays of different wave lengths is always *remarkably constant*. It has a weakly acid reaction, a pH of 6.6 (6.50–6.77). Fink (1925) in *Pieris rapæ* found greater variation at different stages: 6.4 for young larvae, 6.2 in mature larvae, 5.9 for early pupal stages, 6.4 for the late pupal stage, but how extensive were his data and whether they have any bearing upon the action of light do not yet appear.

We are thus still without perfectly satisfactory proof that the activity of tyrosinase in butterfly blood is conditioned by the action of light, but the evidence furnished by Brecher points in that direction. Ultra-violet rays seem not to affect it; they promote rather than retard the action of tyrosinase upon tyrosin during the sensitive period of larval life when internal metamorphic changes are most rapid. Yellow rays prevent the melanic reaction and allow green pigmentation to develop. Whether an enzyme exists which promotes the formation of green pigment or whether the variable green is a highly modified derivative of chlorophyl are questions which we cannot yet answer.

The question was raised by Mendola (1873) and by Poulton (1887) whether these pupal color adaptations were produced through the eyes and nerves or by the direct action of the light upon the skin of the larva. Poulton (1887) covered the eyes of caterpillars with black varnish just previous to the sensitive period and

got negative results, leading him to believe that the light acts directly on the skin, not through the eyes. But Przibram (1922) found that by cauterizing the eyes or cutting off the whole head he got the same results as in darkness, whatever the surroundings, that is, the action of the light upon the skin is indirect and through the eyes. Brecher (1924a) similarly found that by coating the ocelli of the caterpillars with transparent yellow varnish, the pupæ became green in *Pieris brassicæ*, golden in the Vanessidæ; when blue varnish was used dark pupæ were the result, as when the insect is kept in blue surroundings. When yellow or blue varnish was used, the nature of the surrounding light became a matter of indifference. The light of long and of short wave lengths thus exerts a differential action only through the ocelli of the mature caterpillar and apparently by nervous control, rather than by direct action through the skin; the mechanism of this nervous control is still unknown.

Dürken (1923) studying *Pieris brassicæ* came to similar conclusions as regards the effect of orange light in preventing the development of black and white pigments, thus allowing the yellow-green pigment to become evident. He found, moreover, that the green color acquired by pupation in orange light, was transmitted to the next generation when pupating in non-colored surroundings; only 7 per cent of a normal control culture pupating in colored environment were green, 93 per cent white and black. The effect of having exposed the parents to orange light was greatly to raise this proportion of 7 per cent. This effect, moreover, was cumulative, for after two generations of exposure to orange light practically every individual descendant, pupating under normal non-colored conditions of illumination, was green. The hereditary transmission of the green (which is essentially the suspension of the melanic reaction) is described as plasmogenetic, or "hologenetic plasmatic induction." The plasma or cytosome of the green cell is affected but not the nucleus.

An objection which might be raised to these experiments of Dürken is that they were mass cultures. The progeny of individual females were not segregated but considered *en masse*, but it is doubtful if more exact methods would have changed the general result.

LIGHT AND WING COLORATION

Little is known about the morphogenetic or physico-chemical effects of light upon wing coloration. Negative results were obtained by Standfuss (1896); Weismann (1895); Kathariner (1900, 1901). Von Linden (1899) observed that *Vanessa urticæ* and *V. io* raised under red glass were in general brighter than the others; those under green, darker; those under blue, paler.

Cholodkovsky (1901) described three aberrant specimens of *V. urticæ* which he obtained out of about fifty bred under yellow or under blue glass. The two bred under blue glass showed an incomplete development of the scales of the hind wings (in one case elongated and hair-like, similar to those of the posterior margin). One could easily pick out of a large series of *Colias eurytheme* or *C. philodice* diseased specimens which show a similar incomplete development. The other aberration, bred under yellow glass, was evidently a melanic, healthy individual with certain spots suppressed; but there is no evidence whatever that it would not have appeared if it had been raised in normal white light.

The general objection which must be raised to all such experiments which do not rule out, or take into consideration,

hereditary factors is that they prove nothing. Large broods of butterflies, especially if inbreeding has been going on, frequently provide aberrations which are seized upon by the experimenter in search of variations as results of external influences; whereas they are due to the interaction or mutation of hereditary factors.

Experimentation should take a new direction and rule out hereditary factors. This can be done, in study of direct action on the wing, by unilateral treatment, exposing to the light to be tested one side of the body only, leaving the other as a control. When one remembers that in certain localities in South America the butterflies of different groups resemble one another surprisingly in their hue, so that as the traveller passes from one region to another he comes upon characteristic local types of coloration, the possibility of light playing some rôle along with food and moisture in the hæmal or cytoplasmic control of development deserves study. We have too long been content with explanations of these interesting phenomena by natural selection. However well or poorly this theory is supported by facts, it tells us nothing of the metabolic processes, the physiological responses of the living organisms with which we are working, to which primarily we must look to learn why and how specific forms and colors are what they have become.

Preliminary to this experimentation one must inform himself about the nature of structural, as well as pigmental colorations. An important contribution to the morphology of structural colors has been made by Süffert (1924), who has described the scales of the butterfly's wing with great thoroughness, amplifying and at some points correcting the work of Onslow (1923) and earlier writers.

ACTION OF TEMPERATURE. SEASONAL CHANGES IN COLORATION

The rate and the extent of the various processes of butterfly metabolism, as expressed in coloration of caterpillar or chrysalis or butterfly, are strikingly under the control of temperature. Coöperating, however, with low temperature, as winter approaches in high latitudes, are weakened illumination and the shorter day. Reduced heat and light stunt growth, diminish the brilliance of certain colors and, within certain limits, promote the development of melanic pigmentation. Moreover, the whole mechanism may come to a standstill, feeding cease, the heart beat rarely or not at all, when the caterpillar, pupa, or adult goes into hibernation.

It is well-known that true melanism is the result of the oxidation of certain products of katabolism (tyrosin, dioxyphenylalinine = "dopa") through the action of one or more ferments, e.g., tyrosinase, and that this action depends very much upon temperature. A high temperature (80°C. for example) destroys the tyrosinase *in vitro*, whereas moderate cold (e.g., 10°C.) favors its action.

The statement that melanism is brought about by a certain degree of cold, corresponding to out-door temperature of autumn or early spring in north temperate latitudes, needs qualification by emphasizing the fact that not all black pigments of butterflies are physiologically alike or, probably, chemically alike. The black variety, "*glaucus*," of *Papilio turnus*, the common yellow swallow-tail of the United States is, as is well-known, found only in the warmer southern states. Cold can have nothing to do with its origin. Similarly, in the classical example of seasonal polymorphism in

Europe, *Araschnia levana-prorsa*, the dark-brown, almost black, variety occurs in the summer generation.

New light has been thrown on this case of seasonal polymorphism by recent studies of Fritz Süffert (1924), who draws a distinction between the physiological effect produced when individuals of the summer generation, which should normally become the very dark *prorsa*, are acted upon by cold as caterpillars or, on the other hand, as chrysalids. In either case the results are similar, that is, a large proportion become the reddish-yellow spring form *levana* or intermediates, and the stimulus, lower temperature, is the same; but when *caterpillars* are treated, the whole course of development is retarded and prolonged ("latent Entwicklung" of Weismann), whereas *chrysalids*, after refrigeration and the return to normal temperature, continue their development at normal velocity ("subitane-Entwicklung" of Weismann). In the latter case we have merely local action upon substances concerned with wing coloration; in the former a general effect upon the rate of metabolism of the whole body.

Süffert has found that the period of susceptibility of the *pupa* to cold is limited to the first twenty-four hours after pupation, and that the susceptible period for the hind wings is in advance of that for the fore wings (maximum effect at twelve hours rather than twenty-four).

Süffert holds, as did Weismann, that it is not low temperature primarily which turns the progeny of *prorsa* into *levana*, for *hibernating* pupæ invariably produce the spring form, *levana*, even when kept in a *warm room* and, so far as known, even when the chrysalis is exposed to heat during the period of susceptibility. Cold affects primarily the rate of metabolism and development rather than the chemical elaboration of pigments. Heat applied to offspring of the summer generation forces on development, resulting in a large proportion of *prorsa* which eclose before winter and within a few weeks.

Süffert's experiments show that the extent of modification of *prorsa* into *levana* depends upon the velocity of individual development, as indicated by the time of eclosion; the slower the individual development the greater is the modification into *levana*. For example, mature caterpillars were exposed to +5°C. during the last days before pupation and after pupation *immediately* brought into a warm room at about 20°C. The sensitive period of the *chrysalis* was thus passed in the warm room, but nevertheless a few *levana*-like individuals appeared among those not modified, and in the following order. The first butterflies to appear were normal *prorsa;* the rest eclosed 1, 2, 3, and up to 8 days afterward, and the later they eclosed the more were they like *levana*. Some individuals indeed did not eclose the same season, their development becoming completely "latent," using Weismann's term for the tendency to hibernate. The others were "incompletely latent" and in varying degree. It remains to be proved whether a hereditary rhythm exists, that is, if climatic conditions were exactly stable, there would still be an alternation in successive generations.

Almost as much difference occurs between the seasonal varieties which succeed one another in the *alfalfa* butterfly, *Colias eurytheme*, of Western and Central United States as in *Araschnia levana-prorsa*, though in the former the color pattern is unaffected. But an extraordinary difference in size occurs between the spring variety, *ariadne*, and *amphidusa* (or *eurytheme* proper) of the summer. The autumn brood, growing while the days are becoming cooler and shorter, is intermediate, and is called var. *keewaydin*. The

changes in coloration consist in the different degrees of elaboration of orange pigment in the yellow scales providing the ground color of the upper sides of the wings. In the little *ariadne* the orange is much paler than in the large brilliant *amphidusa*, this difference being more striking in the male, which is always more highly colored, than in the female. It has usually been assumed from Hopkins' (1895) studies on the yellow pigments of Pieridæ that they are all purine products, though it should be remembered that the color of the various well-known compounds of uric acid is white. The chemical nature of the orange pigment, and of the orange reaction induced in the blood flowing into the scales of the wing bud at midsummer temperature, are matters deserving further investigation.

The melanic pigmentation of individual scales of the under sides of the hind wings and tips of the fore wings varies inversely with the orange of the upper surfaces, that is, in the summer brood this melanic pigment does not appear except in rare strains in which it is under the control of hereditary factors. Thus, from four brother-sister matings of *philodice* made during the first week in June, 1920, four families eclosed in July, all bred under the same conditions as to temperature. Broods ι, λ, ο were hereditarily swarthy, whereas *s* was a large brood of 245 adults of typical summer coloration. Brood ι consisted of 253, λ of 133, ο of 281 individuals. No quantitative study in these three broods of the individual variation in melanism, which is considerable, has yet been made, but as a whole these broods are very conspicuously melanic as compared with brood *s*.

It was for a time my belief that the width of the black wing-border of the male of *Colias philodice* and *C. eurytheme* is narrower in the fall generation. Families raised in the fall have in many cases been characterized by extraordinarily narrow marginal bands, and it is difficult to determine by mere inspection and comparison with the male parent that this is not in part a seasonal effect, the width of the band being subject to much individual variation; but the corresponding females do not show a proportional narrowing of their marginal band. The width of the band is certainly in general inheritable, and the fall broods showing exceptionally narrow bands were produced by close inbreeding, so that I must conclude, until careful quantitative studies have been made, that the melanic border of the upper side of the wings is not essentially affected by heat and cold.

It is especially the under side of the wings of butterflies, as, for example, in the small blue Lycænid, *Pseudargiolus lucia-neglecta*, which is particularly subject to seasonal changes in melanism. The oxidation taking place in the tyrosin-tyrosinase reaction and the production of melanism is promoted by the exceeding thinness of the membranous diaphragm separating the scales of the under side of the wing from the underlying air cavity, thus allowing the air to come into close contact with the scales. The cuticle of the wing bud immediately covering the upper surface of the fore wing, however, is much thicker and probably impervious to oxygen, which accordingly reaches the developing scales of the wing-surface between the nervures only internally through the tracheæ, so that there is less oxidation and less elaboration of melanin on this upper surface, except for those markings of the color pattern which will be described later.

Caterpillars of *Colias eurytheme* show an interesting seasonal melanic variation. In certain strains bred in the fall and winter two dorso-lateral rows of squarish black

spots appear. A pair of them occurs close to the posterior margin of each segment, apparently just over the lateral margin of the pericardium (fig. B).

Nothing is known of their heredity, and since nothing exactly corresponding to them is ever seen in the summer generation it would not be possible to follow the course of their transmission, which may be very irregular like that of the bright-colored dorso-lateral lines in *C. eurytheme* caterpillars, on which I have a series of unpublished data, or like the gray-black and the green larvæ of the "Elephant

Fig. B. Seasonal Melanic Variation in Caterpillars of the Alfalfa Butterfly, *Colias eurytheme*

Black dorso-lateral spots appear only in late fall and winter.

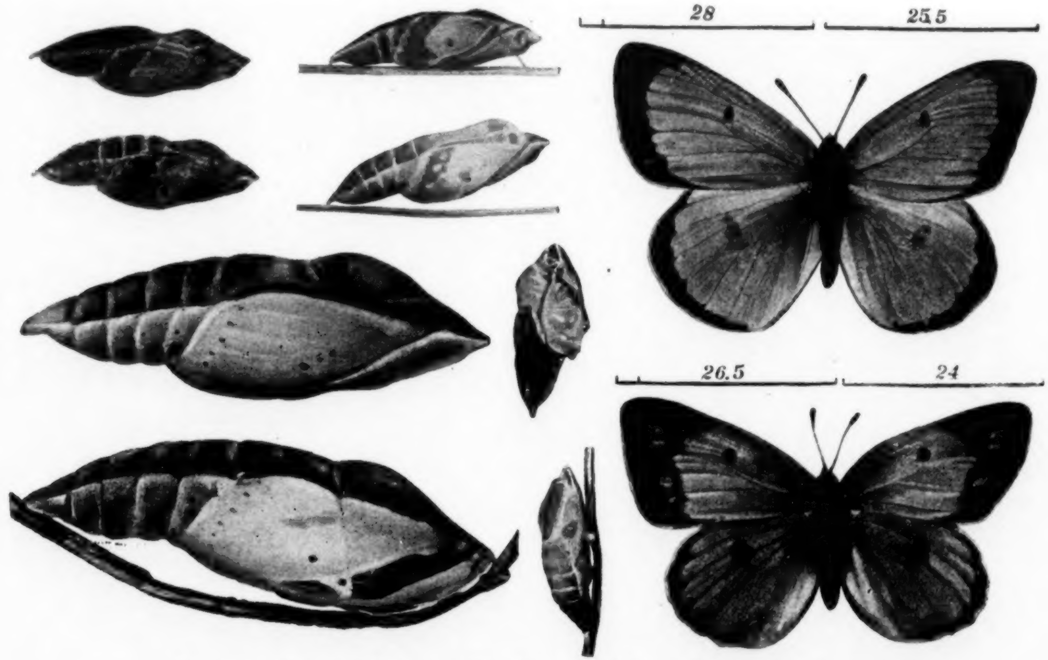
hawk moth," *Chaerocampa elpinor*, which Federley (1916) regards as belonging to one biotype, one hereditary pattern.

THE PHYSIOLOGY OF MELANIZATION AND OF A SIMPLE COLOR-PATTERN

The wonderful variety of form and color in the patterns upon the wings of butterflies is so familiar to us and so appealing to our love of the beautiful that it probably seldom occurs to one that each pattern and even the localization of each spot and band has its physiological meaning. But until recently little effort has been made to assign any other meaning to these patterns than that of protection against enemies, chiefly birds, which were thought, and in fact known, to eliminate individuals not especially protected. If a butterfly could be shown in a small minority of cases to resemble a leaf or bark of a tree, or to have an odor faintly disagreeable to mankind, or to resemble another accused of having such an odor, we have been content to think that natural selection would somehow account for color patterns generally. Yet we have always recognized that natural selection, which remains the only theory which we have of the origin of adaptations save the still poorly-supported Lamarckism doctrine of direct environmental action, depends upon variations about the origin of which we have known next to nothing.

It is the recent advances in the study of variations, knowledge of to what extent and how they are inherited, and especially the physico-chemical mechanism of their development in the individual, which are the hopeful signs of progress in the science of evolution. When we can understand by the help of physics, chemistry, embryology and ecology how even the simplest organism takes on the patterns which it assumes during its span of life, we shall have taken the next essential step in the study of evolution.

So it has seemed to me that, in beginning the investigation of the origin of the wing patterns of butterflies, we should choose one that is very simple and which depends upon chemical processes of pigmentation about which something is already known. Such a wing pattern is that of *Colias philodice* and its near relative *Colias eurytheme*, consisting of a simple black border (narrow and unbroken in the male, broader and usually splashed with spots of the yellow ground-color in the female) and a black "discal" spot in the middle of



RELATION OF CUTICULAR PITS IN THE WING BUD TO THE MELANIC BORDER AND DISCAL SPOT

Figs. 1, 2 (Upper left, top row). Mature male pupæ, showing blackened pits at the edge of the black border of the underlying wing and close to the black discal spot. Figs. 3, 4 (Upper left, second horizontal row). Same, in mature female pupæ. Fig. 5 (Third horizontal row, extreme left). Young pupa, showing just-blackened pits in the cuticula before development of pigmentation in the wing. Fig. 6 (Fourth horizontal row, lower left corner). Cast pupa-case, showing blackened cuticular pits. Figs. 7–10 (Four figures at right). Effect of closing with bees wax the pits in the right wing bud of young pupæ. Fig. 7 (Center of plate). Cast pupa-case of a male, showing wax over the pits. Fig. 8 (Upper right corner). Same male butterfly; effect of closing pits on right wing bud of pupa; note small modified right wing, shortened 2.5 mm. Fig. 9 (Bottom row, middle). Cast pupa-case of a female, wax-covered pits. Fig. 10 (Bottom row, right corner). Same female, right wing shortened 2.5 mm.

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each fore wing. What determines the position and extent of these deposits of melanin? Why is the border broad and irregular in the female, narrow and solid in the male?

The clue to the answer to the former question was soon found in the presence of a minute pit in the cuticula at the middle of the pupal wing bud. Its walls blacken almost immediately after pupation. Spreading backward from this point, about a week later, the black discal spot of the wing itself develops beneath the thick but transparent cuticula. Similarly a row of minute cuticular pits, connected usually by a furrow, run parallel to the margin of the wing-bud immediately above the edge of the future wing.

It is from this row of pits, which blacken immediately after pupation before the soft, freshly-secreted cuticula has hardened, that the marginal band of the underlying wing is later to develop, extending inward toward the middle of the wing. The yellow pigment in the scales of the general surface is already formed while the marginal band and discal spot are still in a transparent, colorless stage. Thus the position of the marginal band is determined at an early period, and it was imagined that an exchange of oxygen and carbon-dioxide might be taking place through the pits and extending over the future melanic areas. To test this hypothesis, I blocked the pits of many pupæ with bees-wax immediately after pupation, in some cases before the cuticular pits themselves became blackened. Closure of the pits, however, did not suppress the black marginal band, which developed in all cases normally, but it evidently interfered with metabolism and checked the growth of the wing, so that, in almost every individual, the wing thus treated became shortened, as compared with that of the other side which was left untreated as a control. The oxygen necessary for the melanic reaction must accordingly have come from the thorax through the tracheæ. I am led to think that the pits are respiratory and serve for the escape of carbon dioxide from the following evidence: the blackening of the pits while the cuticula is still soft, the colorless areas of scale-bearing epithelium beneath them where yellow pigment does not form but which eventually blacken, and the stunting of the wing when the pits are closed. Incidentally this throws light on a question which has puzzled students of the physiology of insects, viz., how is carbon-dioxide eliminated.

It is possible, and indeed probable, that the central pit of the pupal wing represents the suppressed spiracle which fails to develop in the mesothorax of the caterpillar, for through the translucent wall of the larval thorax one observes that the line connecting the spiracles crosses the middle of the wing bud. In some individuals a slight depression is visible in the mesothorax at the point where a spiracle ought to be. The suppressed spiracle, involving a cuticular pit permeable to gases, probably determines, therefore, the position of the discal spot in the wing-pattern of the butterfly. The marginal band of the butterfly's wing can similarly be traced back to a submarginal bundle of trachioles in the wing bud of the caterpillar, which corresponds in position to the submarginal row of pits and the connecting furrow in the pupa.

Thus the simple wing pattern of this butterfly probably owes its main features to details in the respiratory system of the caterpillar's wing bud.

There are many unsolved problems about the determination of the wing pattern in *Colias*. How can we explain the greater width and more diffuse inner

margin of the melanic border in the female as compared with that in the male? Experiments looking toward the solution of this and other questions are not yet far enough advanced to be reported at present, but new methods have been devised which promise more accurate knowledge of wing color and pattern.

Onslow (1916) has studied the chemical basis of the black markings on the wings of *Pieris brassicæ*. The immature fore-wings were dissected out of a number of pupæ and placed for twelve hours in watch glasses containing (1) saline solution, (2) hæmolymph (from crushed pupæ ground up with kieselguhr and chloroform water), (3) saturated tyrosin solution.

A wing kept in normal salt solution turns slightly black, but if previously boiled it remains uncolored.

A wing placed in hæmolymph turns black even if previously boiled, but if both wing and hæmolymph are boiled it remains uncolored.

In saturated tyrosin solution a wing turns extremely black, but if a wing is previously boiled it remains uncolored.

The conclusion is reached that both the wing and the hæmolymph, respectively, carry both tyrosin and tyrosinase, since blackening occurs when the wing is placed in hæmolymph unless both wing and hæmolymph have been previously boiled. Both chromogen and tyrosinase adhere to the surface of the wing and to the surface of the scales, but whereas white pigment is found (in white areas) on the surface, the black pigment permeates the chitin of the scales. In his general conclusion Onslow holds that the localization of the black area is due to the *restriction of the tyrosin to the black areas*, while the tyrosinase is everywhere present, for when the wing is placed in a tyrosin solution it becomes black all over, but when it is placed in a tyrosinase solution the darkening is restricted to the markings. Thus the form of the markings is determined by the localization of the tyrosin in these areas, and oxidation takes place as soon as the atmospheric oxygen has access to the surface of the wing.

PIGMENTS IN THE BLOOD AND THEIR ORIGIN

Although all butterfly pigments are in last analysis blood pigments, few of them give color to the hæmolymph. Melanin is produced directly in the blood only when the latter is drawn and exposed to oxygen of the atmosphere. The white and yellow wing pigments of the Pierids, usually regarded as products of uric acid since Hopkins (1896) found that they give the murexid test, are deposits left by the blood within or upon the scales. A third group of pigments, possibly derived without much chemical change from food-plants, color the hæmolymph green or yellow.

The best known of these are the yellow carotinoids, which in birds and mammals are associated with fats or lipoids. If leaves of plants and vegetables containing carotin are omitted from the food of a fowl, the yolks of the eggs which she lays become pale, being deprived of the yellow pigment, carotin, which is ordinarily absorbed in digestion of green plants. In certain breeds, e.g., the white leghorn, this pigment appears in the ear lobes and legs, as well as in body fat and blood serum. Since it is gradually used up during egg-laying, the legs of good layers become progressively paler, whereas those of poor layers remain bright yellow. Butter from cows at pasture is bright yellow, from cows deprived of fresh green food it is paler. The yellow pigment of the corpus luteum, body fat, and blood serum in mammals is known to be carotin.

Carotin is a highly unsaturated hydro-

carbon. As extracted from carrots, it has the formula $C_{40}H_{56}$. Xanthophyl is its dioxide, $C_{40}H_{56}O_2$.

Meldola (1873) first suggested the idea that the green color of certain insects is due to the absorption of chlorophyl from the food mass in the intestine, with slight modification, into the hæmolymph.

Poulton (1885, '86a, '86b, '87, '93) in a series of interesting papers made a distinction between those pigments which are formed within the tissues of leaf-eating larvæ ("endogenous," Verne, 1925) and those derived from the food ("exogenous"). "The derived pigments often occur dissolved in the blood, or segregated in the subcuticular tissues (probably the hypodermis cells), or even in the chitinous layer, closely associated with this cuticle itself."

It was clearly brought out by Poulton that the digested pigments undergo extensive and very diverse chemical changes in their absorption into the blood in different caterpillars. They become associated with the proteid of the blood or tissue. When alcohol is added to the hæmolymph of the buff-tip moth, *Pygæra bucephalus*, the proteids are precipitated, carrying with them the chlorophyl which soon disappears, leaving the carotin ("xanthophyll") in solution. Palmer (1922) says of this "If the affinity of carotin for blood protein, as found in some cases for mammals, is a universal property of this pigment, these results of Poulton's on the hæmolymph of caterpillars lend support to the tentative conclusion that the chief carotinoid of the larvæ and pupæ of butterflies is carotin."

The view that the green and yellow blood pigments of certain green caterpillars are derived from chlorophyl and carotin of their food, though very generally held, has not been adopted by Przibram and Brecher. Przibram (1913) found that, by heating the ether solution of the pigments of certain green animals (green grasshoppers, *Cantharides*, the frog) with an equal quantity of alcoholic solution of potassium hydroxide, a yellow precipitate is formed and the solution becomes clear, in contrast to the extract of plant pigment, which remains green and turbid. Upon application of more potassium hydroxide and heat, a still more striking difference appears: the extract of animal pigment remains clear after the formation of colored precipitates while that of the plant pigment remains cloudy and contains a black precipitate. Concentrated sulphuric acid applied to the ether solution of "animal green" gives a wine-yellow color, becoming brown, whereas the plant extract remains green. Nitric acid decolorizes the animal extract, while that from plants remains green or fades out slightly into yellow.

These reactions are such as one would expect if the various animal pigments are associated with proteins, as they certainly are in the hæmolymph of Lepidoptera, and if those extracted from leaves are relatively free from such albuminous substances. These reactions present no reason for uniting together in one category ("Tiergrün") all green animal pigments nor for claiming that none of them may be a compound derived directly from chlorophyl. No one would imagine that the green pigment of the carnivorous frog, or of the mantis, grasshopper, or, in fact, any of the Orthoptera, can have their immediate source in chlorophyl, but one may hold an entirely different opinion in regard to some of the green pigments in caterpillars. The well-known experiments and observations of Poulton (1885, 1886a, 1886b), point in this direction, especially those on the larvæ of the moth *Tryphæna*, which, after feeding normally on leaves of cabbage containing chloro-

phyl or etiolin become green or brown, but which, deprived of food containing either, and kept alive by feeding on the mid-ribs of cabbage, lack altogether the green and brown pigments of the body wall.

This experiment, however, in my opinion, is not wholly conclusive, though it is perhaps the best experimental evidence which we have that the grass-green pigments of the blood and body-wall of leaf-eating caterpillars are derived from chlorophyl. The principal objections to the experiment as described are that we are not informed that the hæmolymph in *Tryphæna* is green or pigmented; the single caterpillar which survived after being deprived of food containing chlorophyl was extremely small (about one-fourth the normal length), its growth being greatly stunted; if the green and brown pigments are truly endogenous, rather than derived from chlorophyl, the stunted growth may have interfered with their development; of the other caterpillars, fed on chlorophyl, only two of the last twenty-three survivors were green, the remaining twenty-one brown. The brown pigment of the body wall is hypodermal, however, and very evidently of a different origin from the typical *cuticular* melanic pigmentation. The further evidence adduced by Poulton (1885, 1886) that chlorophyl is the source of these green and brown pigments rests chiefly on comparisons between the absorption bands in the spectra of the hæmolymph of green caterpillars and of green leaves. A corresponding absorption band occurs at the red end (70–65) and another (around 50) in the green. In the leaf, however, two additional fainter absorption bands occur in the intermediate region (63–61 and 60–57.5) which have no counterparts in the spectra of the hæmolymph exhibited. Poulton's observations bring out of the fact that the problem is complicated with other factors both hereditary and environmental, which coöperate to determine the green and brown pigmentation of caterpillars, acting as he believes, upon the variable raw materials (exogenous pigments) from the food-plant. The larva of *Sphinx ligustri*, for example, is dull-colored if fed on lilac, bright-colored when fed on privet. The argument in favor of derived green pigments seems also somewhat weakened by the case of *Sphinx ocellatus* (Poulton, 1886, p. 169), in which the blood is only faintly tinged, while the body wall is deeply colored. Thus the blood "cannot produce any effect upon the larval appearance until it has been collected in the superficial cells." The blood is regarded as the medium by which the pigment is slowly transferred to the body-wall. "Before pupation the pigments are withdrawn from the cells and are dissolved in the (pupal) blood. . . ." "Such conclusions render it probable that the most complete demonstration of the vegetable origin of the derived pigments will be a matter of great difficulty." Nevertheless, the experiment on *Tryphana* reported several years later was regarded as conclusive.

The evidence in regard to the transfer of carotin of the food plant to animals is more extensive and satisfactory than that in respect to chlorophyl. It has been summarized by Palmer (1922) in his book on "Carotinoids and related pigments." Knight (1923) and Palmer and Knight (1924) have recently reported that the double-eyed soldier bug, *Perillus bioculatus*, owes its yellow and red colors to carotin derived from the blood of the larvæ of the potato beetle (*Leptinotarsa*), which in turn get it from the leaves of the potato plant. Under low temperatures (65°–75°F) a large amount

of this pigment becomes deposited in the body wall, whence red or yellow variations arise; on the other hand, at high temperatures (85°–95°F) large amounts of it are oxidized and destroyed, so that white variations appear in the nymph.

HEREDITARY CONTROL OF A CAROTINOID PIGMENT

An interesting case of the mutations of grass-green into blue-green caterpillars through the action of a simple mendelian recessive factor, which apparently destroyed the normal carotinoid pigment, first appeared in my cultures of *Colias philodice* in August 1920. The stock had descended from a single female butterfly, the progeny of which had wintered as caterpillars. Inbreeding had then occurred for two generations. The caterpillars which hibernated and those of the following (June–July) generation were all of normal grass-green appearance, but in the August generation forty-four conspicuously blue-green individuals appeared in broods containing three times that number of normal larvæ. Evidently the parents of the three particular broods showing this ratio were grass-green heterozygotes for the recessive blue-green factor. Thus one member of the original wild pair of butterflies of the previous autumn must have been heterozygous for the recessive blue-green factor, the other mate being a normal grass-green dominant; and the same sort of combination must have occurred in both of the brother-sister pairs of the spring (early June) generation; their offspring were also all grass-green but 50 per cent were probably heterozygous for blue-green, for from them came the heterozygous butterflies belonging to the summer (late July) brood which, mating together, produced blue-green caterpillars. Other pairs of their brothers and sisters, one or both of which were homozygotes for normal grass-green, produced only grass-green caterpillars.

Unfortunately for the purposes of experimental breeding, the recessive blue-green butterflies, though strong and healthy, seldom would mate together, owing to sterility, especially of the male; however, a mating of this sort was once obtained and blue-green caterpillars only were the result.

The butterflies developed from blue-green caterpillars which survived the winter of 1920–1921 failed as usual to mate, but fortunately several females which wintered as grass-green caterpillars were the offspring of a pair of grass-green parents of which the male was known to be heterozygous for blue-green, for, by another mating, he had produced some blue-green caterpillars. These females, of which one half, though grass-green, were heterozygous for blue-green, were mated early in May with wild males. Inbreeding in one of the families of the second generation (June–July) gave again in August most extraordinary results. In three families another mutation or variety which I had never seen, caterpillars with olive-green skin, appeared with the double dominant grass-green and recessive blue-green in the ratio: 9 grass green, 3 olive, and 4 blue green. Four other matings produced 314 grass-green and 128 olive caterpillars.

Olive when homozygous for the recessive reddening factor b, (which adds a reddish element to the pigment in the hypodermal cells of the larval skin and of the eye, and tinges certain wing scales of the butterfly with orange) breeds true to olive; a pair homozygous for olive but heterozygous for blue-green (a), viz., Aa bb, throw 25 per cent of aa bb, blue-green, olive being the epistatic color. Doubly heterozygous grass-green individuals, Aa Bb, mated together gave the

9:3:4 ratio mentioned above. The "olive" butterflies, unlike the "blue-green" and especially the male of the latter variety, showed no particular signs of sterility, and were strong and healthy. That is, the olive individuals were as easily mated and laid as well as the grass-green individuals of the same cultures.

The physiological and ecological characteristics of these two variations are of unusual interest. In both of them the green eye of the adult butterfly showed a tinge corresponding to skin color of the caterpillar from which it developed, that is, either a bluish-green or a brownish tinge, not as abrupt a variation as in larval skin-color but always present in individuals known to have been in their youth blue-green or brown caterpillars.

The blood of the blue-green caterpillar and butterfly was distinctly blue-green, that of the olive, so far as could be seen, normal grass-green. The absence of yellow pigment from the blue-green blood and from the hypodermis of the caterpillar and compound eye affects in no way the pigments of the scales, which are of an entirely different chemical nature from the yellow pigment missing in the blue-green caterpillar. The scale pigment, tentatively at least, is to be regarded as a derivative of uric acid, the other as carotinoid. On the other hand, the olive factor which reddens the normal yellow-green hypodermal pigment into olive-green (a mixture of yellow-green and red) also reddens the scales upon the under surfaces of the hind wings and tips of the fore wings, changing them into orange. The scales of these particular surfaces, as I have indicated in the discussion of seasonal variations, are exposed to a high degree of oxidation, which would suggest that the olive factor may perhaps be an oxydase and the olive reaction an oxidation.

The egg of the female with blue-green blood is pure white, not cream-white as in the normal female with yellow-green blood. Similarly, the cocoon spun by the hymenopterous parasite *Apanteles flaviconcha* Riley, when it passes its larval existence within the blue-green caterpillar and feeds upon the blue-green blood, is white rather than bright golden-yellow, the latter being the color of cocoons spun by these parasites after living on normal yellow-green blood.

The blue-green mutation illustrates in the clearest possible way throughout the whole life history of the insect the absence of a yellow pigment from the hæmolymph and from the hypodermis. Even the pink line, which in the normal larva is traced more or less distinctly along the middle of the lateral white band running through the stigmata, is absent from the blue-green caterpillar.

The fundamental question is: how is the yellow pigment suppressed so that the blood and skin become blue-green? If the yellow pigment is carotin derived from the clover which serves the caterpillar as food, as seems highly probable, and if the chromosome hypothesis of the physical basis of heredity is in general true, then we are led to think that the nuclei of the intestinal epithelial cells and especially their chromosomes, produce some substance capable of destroying carotin during the digestion and absorption of plant pigments through these cells into the blood. This is a most definite case permitting the identification of a hereditary factor with a relatively simple physico-chemical reaction localized in a definite tissue (intestinal epithelium) but, through the blood, affecting other tissues, especially the hypodermis.

The alternative hypothesis, favored by Przibram, is that the yellow pigment is a

"lipochrome" of unknown chemical nature formed within the hypodermal cells and possibly other cells, from which the blood takes it up.

There can be no doubt about the endogenous origin of the gene or factor for blue-green, the active agent in suppressing the yellow pigment. It appeared spontaneously under normal conditions, except for the close inbreeding, and was transmitted in the simplest mendelian fashion. And until it can be shown that the yellow pigment is not a carotinoid, the former hypothesis is more useful. It is supported by much recent circumstantial evidence in regard to carotinoids cited by Palmer (1922), by Verne (1924) and others.

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GROWTH AND DIFFERENTIATION IN PLANTS

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I. Introduction

When one sees a plant he may be aware only of some striking characteristic, e.g., size, or color, but if he observes he must become aware not only of its specific characters but of a certain relationship between their shapes, sizes, involutions, intricacies, dispersions, contrasts, and diversities. By some these qualities are regarded as puzzling examples of the mystical methods of nature. Others regard them as the expression of forces acting upon the plastic substratum of life to produce organisms having such definite characters as to give one the opportunity to classify them into related groups, species, families, and so on. Furthermore, these characters are unique in being passed on from one generation to another with the result that each individual reaches maturity through a rather uniform series of processes.

This paper will be devoted to a discussion of some of these processes as well as to the characteristics of the mature organisms.

One of the important features of biological processes is their continuity. The organism of today is the organism of yesterday plus or minus a certain number of molecules of water, carbohydrate, and other material. The changes in composition of the cell are wrought, in large part, by enzymes which bring about hydration, dehydration, oxidation, reduction and like changes. These processes go slowly in comparison with many chemical reactions *in vitro*, and are often reversed, but they play an important part in the development of the organism.

The growth of an organism usually begins at a slow rate, gradually increases for a time, then as the organism approaches maturity it goes more slowly and finally no further increases are perceptible. Many chemical reactions proceed in the same way, especially those in which an autocatalyst is concerned.

Our knowledge of the growth of organisms has been immensely advanced in recent years by the application of quantitative methods to its study. Having found that the increase in size of the organism is an orderly change, it is possible to give mathematical expression to it, analogous to those which express chemical changes. Biologists have not yet settled on the general use of any particular algebraic equation to express this relation, perhaps none yet evolved is adequate for the purpose. Their application has however focussed attention upon the orderly nature of the growth process and makes it more apparent that this process is a manifestation of the energy relationships prevailing in other forms of matter.

II. Some Dynamical Aspects of Growth

The successful application of the Verhulst equation to biological data by Pearl and Reed (1922) has attracted no little

attention. The equation appears to lend itself readily to problems of population and to other statistical enquiries.

$$y = d + \frac{k}{1 + me^{a_1x + a_2x^2 + a_3x^3}}$$

here, y = population at time x; d = total growth attained in all the previous cycles; k = the upper limit of growth, or the value of y at infinite time; m = an arbitrary constant of time.

In my own work I have made frequent use of the equation for autocatalysis which has served admirably to analyse the growth processes of organisms. Other equations may be as good, or better, but one must use the tools at hand until better can be found. We may give attention to the equation as commonly used:

$$\log \frac{x}{A-x} = K(t - t_1)$$

in which x is the size of the organism at time t; A is the maximum size attained at maturity; K is a constant; and t_1 is the time at which the organism is half grown, i.e., where $x = \frac{A}{2}$. Those who are interested in the derivation of this equation may consult Robertson (1923).

In another place (Reed, 1924b) I have enumerated a number of organisms for which this equation has been found by trial to express the growth.

The value of K (the specific constant of growth) appears to have reality in the examples which have been studied. We may consider the growth rate of sunflower plants which were arranged for purposes of study into four groups according to their heights at maturity (Reed, 1919). Table 1 shows that the average final heights of plants in the four groups were quite variable, ranging from 198 to 312 cm., though the values of K were remarkably constant. The fact that the mean values of K are within the range of their probable errors may be taken as evidence of a specific velocity constant in the plants of the four groups. The dispersion of the growth constants from their means, as measured by the standard deviations, of the larger plants was wider than that of the smaller plants.

TABLE 1

Height and growth constants of sunflower plants

	QUARTILE			
	I	II	III	IV
Mean final height of plants at maturity	198 cm.	238 cm.	272 cm.	312 cm.
Mean value of K	0.0440 ± 0.0011	0.0421 ± 0.0016	0.0429 ± 0.0017	0.0443 ± 0.0023
Standard deviation of values of K	0.0052 ± 0.0008	0.0079 ± 0.0011	0.0079 ± 0.0012	0.0111 ± 0.0016

If the foregoing assumptions concerning the specific velocity constant are correctly taken there must be something else which determines the final size of the organism. Gaines and Nevens (1925) have made the interesting suggestion that A/K is a specific constant representing final "growth capacity." Its value as an index of growth capacity depends upon the association between the length of time that the crop, or one of its constituents, continues to grow, and the final extent of growth. This obviously ought to follow and the authors found evidence for the correctness of the assumption with the plants they studied.

A brief experience with growth curves of organisms will show that cylic or periodic growth is common. In man there are three post-natal cycles of growth, infantile, juvenile and adolescent. These cycles overlap to some extent and it is often impossible to discern their exact limits. Indeed, the more we know about them the less reason we have to expect that they have any well marked boundaries. The quantitative treatment of these cycles presents certain problems, but none are necessarily insoluble.

The existence of intra-seasonal cycles of growth in the shoots of certain trees, has been shown to be quite independent of definite fluctuations in environmental conditions. A more extended inquiry will undoubtedly show many cases of cyclic growth in plants. Laughlin's (1919) quantitative studies on the periodicity of cell divisions in onion root tips point the way to fruitful investigations.

TABLE 2

Comparison of the constants of the curves for intra-seasonal cycles of growth of apricot shoots

	CYCLE		
	I	II	III
K	0.0380	0.0355	0.0277
k	0.000344	0.000509	0.000605
$\frac{A}{K}$	2895	1964	1653

The measurement of a population of shoots on young apricot trees (Reed, 1920a) showed three definite cycles of growth, each conforming to the type of growth curve above discussed.

The first cycle covered the period from 0 to 8 weeks, the second from 9 to 17 weeks, and the third from 18 to 28 weeks, dating time from April 20. The values of A for the three cycles were taken as 110.4, 69.7, and 45.8 cm.

The correspondence of observed and calculated values was satisfactory in each cycle. The values of the growth constant K showed comparatively little variability in the three cycles, but those of k were less constant, (table 2). The progressive decline in the values of $\frac{A}{K}$ may indicate, as Gaines and Nevens (1925) have suggested, a progressive lowering of the growth capacity of the shoots.

There seems to be little chance for doubt that these fluctuations in the rate of elongation have a real physiological significance. Certain aspects of this problem have already been published (Reed, 1921a) in which I showed that sap concentration and growth seemed to be inversely related. When growth was rapid the concentration (measured by the freezing point depression) was less, and *vice versa*. Expressed in the form of a coefficient of correlation I obtained values of r approximating -0.600.

Reverting to the nature of the growth process in this population of apricot shoots, it seemed worth while to consider another form of growth curve and its mathematical expression. There is a possibility that their growth in length followed the course of a reaction which consisted of two consecutive monomolecular reactions, one of which at first accelerated and later retarded the other. Wilhelmy's equation formed the basis of the attempt from which the equation for the curve was worked out:

$$x = 210\,[1 - e^{-0.055(t-1)}] + 19.1[e^{-0.055t} \cos \frac{\pi}{14} t]$$

This was considered to show that the main reaction (expressed by the first term) was periodically accelerated and retarded by another term (expressed as a function of t involving the cosine). While the assumptions made cannot be pushed too far with the data now avail-

able, it does seem apparent that the cycles of growth had a real existence and that they may be studied as *processes* of some sort.

Additional information was obtained from a study of data on the growth of white rats, which recovered from suppressed growth due to prolonged fasts. Curiously enough, these small starved rats, when given an adequate diet grew to maturity and equalled in size those which had been given adequate diets from weaning (Reed, 1921c). The second cycle of growth of rats recovering from starvation began, and reached its maximum relatively earlier than in the case of rats given adequate diet continuously. Indeed, an equivalent gain in weight was made more quickly in the animals recovering from suppression than in animals on adequate diets.

The existence of cycles of growth may be inferred from the definite way in which laterals are often grouped on the main axis of plants. On a subsequent page there is a discussion of the pattern of young apricot shoots in which it is shown that the size relationships of the primary laterals suggest a distribution in conformity with a curve of cyclic growth. Although this particular instance deals with the static rather than with the dynamic aspects of the problem, the results are compatible with the preceding discussion and justify the assumption that there is a common principle acting in the two instances.

In the light of the evidence briefly presented, showing that there seems to be an orderly, definite growth process resembling in many ways an autocatalytic reaction, it seems logical to discuss the question of growth-promoting substances.

The effect of diffusible substances which have definite growth-promoting abilities may be demonstrated in cases of cell division which follow the isolation of pieces of tissue. A small fragment of tissue containing fibrovascular bundles accelerates the process of cell growth and division. Lamprecht (1918) cut small pieces of leaf tissue (3 x 3 mm.) and placed them upon each other in Petri dishes containing moist sand. Cell divisions occurred only in pieces which contained vascular bundles. However, if pieces with and without bundles were placed one on top of the other, tangential cell divisions did occur, first in the immediate neighborhood of the bundle, later over the entire wound surface. In all experiments the presence of vascular bundles was necessary for the appearance of cell divisions. In the vicinity of the leptome the divisions started first and were more numerous than in the vicinity of the hadrome. The substance which stimulated cell division is not strictly specific, but works between related genera, but not between distantly related genera or families.

The growth promoting activity of the tip of the coleoptile has been shown by a series of decapitation experiments. Söding (1923) cut pieces 3 to 5 mm. in length from the coleoptile tips and accurately measured the length of the remaining organ. The apical pieces were then replaced on certain decapitated stumps and their lengths measured several hours later. It was evident that the replacement of the tips materially accelerated the growth of the coleoptiles and Söding regards the results as evidence that some sort of a growth promoting hormone is produced in the tip which is transferred to the stump by diffusion.

III. STATIC ASPECTS OF GROWTH OF THE PLANT

1. Correlation between age and relative size

Although the growth process has been shown to represent an increase in mass

which is some sort of a function of time, it fails to answer many questions which are of paramount importance in formulating an exact idea of the development of individuals.

If one notes the variability exhibited by a population of plants, especially in a case where growth has ceased, he may properly raise the question of their relative sizes at earlier stages in their development. For example, are the plants which are small at maturity, those which were small from the beginning, and those which are large at maturity likewise superior plants from early life? The question is important not only from a theoretical but also from a practical standpoint. There are several ways of attacking the problem though few biologists have undertaken it.

There is a tendency, especially among those who are unfamiliar with the quantitative investigation of biological problems, to ascribe these differences to the heterogeneity of the environment. That the environment is variable we must admit, yet, after making all due allowance for this cause, there are permanent differences which can only be satisfactorily explained by assuming that they are in some way bound up with the genetical constitution of the plant.

The first and most important work on this problem was that of Pearl and Surface (1915) who investigated the height variations of a population of maize plants during the growing season. Several years later the writer (1919) made a similar study on a population of sunflower (*Helianthus*) plants and obtained confirmatory results. In both studies the height of the plants was measured either semi-weekly or weekly from a very early stage until increase in height ceased. The measurements were assembled so that the plants on each day of measurement fell into quintiles or quartiles.

There was a strong tendency for plants to remain in or near the quintile (or quartile) in which they started. The quantitative expression of this tendency may be derived from a few relatively simple computations. I shall illustrate by use of the data on *Helianthus*. If the quartile positions of the plants at each measurement had been due to the operation of purely random factors, we should expect to have found them in one quartile as often as in another. The theoretical

TABLE 3

Helianthus annuus. Number and percentage of the height measurements which fell in the several quartiles after the original classification into quartiles

Quartile in which plants started	Quartile positions observed during growth of plants								Total number	Theoretical standard deviations	Observed standard deviations
	I		II		III		IV				
	Number	Per cent	Number	Per cent	Number	Per cent	Number	Per cent			
I	68	45.33	31	20.67	28	18.67	23	15.33	150	3.53	11.92
II	26	18.57	52	37.14	35	25.00	27	19.29	140	3.64	7.52
III	42	28.00	36	24.00	47	31.33	25	16.67	150	3.59	4.94
IV	11	7.86	23	16.43	41	29.29	65	46.43	140	3.63	14.60
Total..........	147		142		151		140		580		
Mean per cent....		24.94		24.56		26.07		24.43			

standard deviations of the measurements are given in table 3 and may be compared with the observed values given in the last column.

The figures show that the observed standard deviations were greater in each case than the theoretical. This means that there is some agency operating to cause variability in height in excess of that to be expected on the basis of pure chance. The influences affecting the height of the plants were naturally greater in the case of the quartiles where the difference between the theoretical and observed values was greatest, namely in quartiles I and IV. This may be taken to mean that there is something in the genetical nature of the plants which was more potent in determining their height than the accident of location, and that this influence appears to be most effective on plants in the extreme classes.

Some additional light on the problem is afforded by the study of Harris (1921) in which he determined certain interperiodic correlations of the size of the *Helianthus* plants discussed above. When the measurements are thrown together into quintiles or quartiles, small differences between two individuals are likely to be given as much significance as large ones, provided they are large enough to throw the two individuals into different groups. While it is true that one must make classes in forming a correlation table, there are usually more classes and each individual has a better chance to count for what it really is.

The coefficients expressing the correlations between the size of plants either at antecedent or subsequent stages decreased as the periods became more widely separated in time. The coefficients were positive and constitute evidence that the size of the plant throughout the growth period bears a relation to its size when first measured. When the increments in height at different stages were studied, the coefficients of correlation were not so unanimous in their meaning, since some were positive and some were negative and many were statistically insignificant. However it appears that the increments of successive periods were generally positive and fairly highly correlated when the periods showed actual growth increments. When the periods were separated by any considerable length of time the coefficients were generally insignificant in magnitude and either positive or negative in sign.

The results of the two methods of investigation are essentially concordant in showing that plants which fall initially into the class of "small" or "large"

TABLE 4

Growth and variability of apricot trees measured as cross section of trunk

YEAR	AGE FROM PLANTING	MEAN	STANDARD DEVIATION	COEFFICIENT OF VARIABILITY
		sq.cm.		
1917	1	2.86 ± 0.31	2.09 ± 0.22	73.22 ± 11.24
1918	2	16.51 ± 0.88	5.84 ± 0.62	35.37 ± 4.22
1919	3	55.75 ± 1.68	11.17 ± 1.19	20.03 ± 2.22
1920	4	92.4 ± 2.12	14.04 ± 1.49	15.19 ± 1.65
1921	5	147.0 ± 4.07	27.0 ± 2.88	18.4 ± 2.02
1922	6	193.7 ± 5.4	36.0 ± 3.9	18.6 ± 2.1
1923	7	208.5 ± 6.22	41.2 ± 4.4	19.8 ± 2.19
1924	8	251.8 ± 7.66	50.7 ± 5.42	20.1 ± 2.24
1925	9	282.0 ± 8.47	56.12 ± 6.00	19.90 ± 2.21

individuals, though variable, tend to stay in that class throughout life.

Few students have given attention to the size growth of trees over a period of years, though many have reported on the fruit production. Data have been secured at this institution upon the growth and variability of a population of apricot trees. The area of the cross section of the trunk at a distance of 15–20 cm. above the bud union is used as the index of tree size and has been found to be reliable for this purpose. Each winter the circumferences of the trunks were measured and the area of the cross section calculated therefrom.

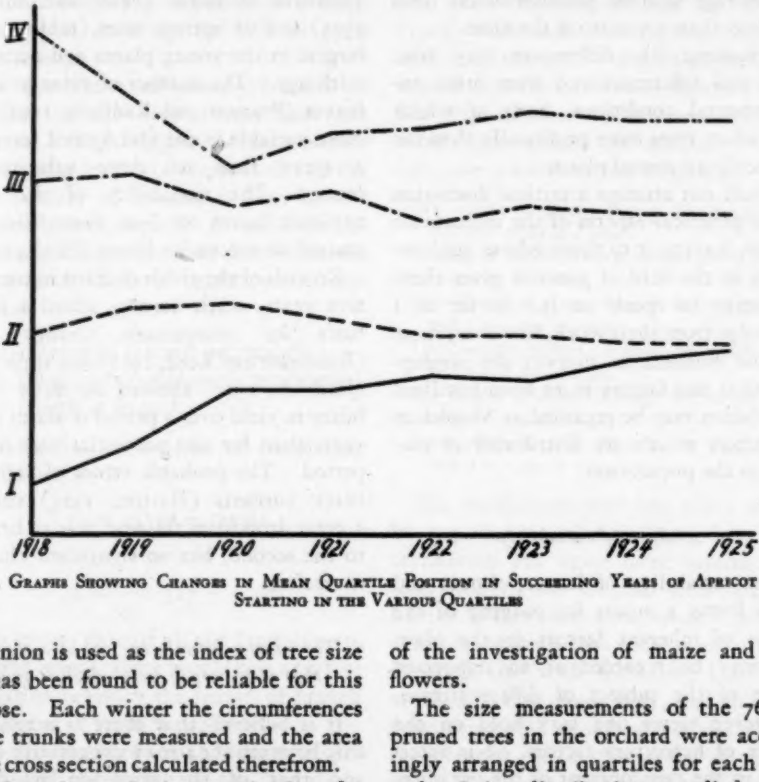

Fig. 1. Graphs Showing Changes in Mean Quartile Position in Succeeding Years of Apricot Trees Starting in the Various Quartiles

Table 4 shows the increase in size of a population of 20 unpruned trees, from the year following that in which they were planted in the orchard. The growth appears to follow the path of a logarithmic curve with the exception of the size in 1923. This lag may be due to the unusually heavy crop of fruit which these trees produced in the summer of 1922. The variability in this population was very high at the outset, but declined in three years to a level which it has since followed rather closely.

For the purpose of the present discussion it is somewhat more important to enquire about the relative size of these trees in successive years after the manner of the investigation of maize and sunflowers.

The size measurements of the 76 unpruned trees in the orchard were accordingly arranged in quartiles for each year and their distribution studied. The graphs in figure 1 show the distribution of the tree measurements in four quartiles of 19 trees each in 1918 and the mean quartile position of the same trees for the seven following years.

The average measurements of trees

whose size gave them a position in quartile I in 1918 were found in the group of smallest trees up to and including 1925, although some of them rose into higher quartiles. Quartiles II and III, the intermediate sized trees, showed relatively small fluctuations from their original values. Quartile IV, which was composed of the largest trees in 1918 retained that characteristic until the end, although the average quartile position of the trees was less than 3.5 most of the time.

Permanent size differences may arise from soil differences and from other environmental conditions, both of which may affect trees more profoundly than the shorter lived annual plants.

I shall not attempt a critical discussion of the genetical aspects of the inheritance of size, leaving it to those whose achievements in the field of genetics gives them authority to speak on it. So far as I can judge from their work, however, there is good evidence to support the assumption that size factors in an open fertilized population may be regarded as Mendelian characters which are distributed at random in the population.

2. *Age and variability*

The variability of leaves, shoots and fruits forms a means for judging of the action of inherent factors in the plant and may be regarded as an important phase of the subject of differentiation. Whatever views one may hold on the nature of hereditary factors, he is interested in the development of the organism produced.

The results of measurements of different characters are not so concordant as to express any pronounced relationship between age and variability in plants. Too many times the measurements have been made on some rather unimportant character and the plant as an entity has been disregarded.

The size of plants, annual or perennial, is generally more variable when young, though I found (Reed and Holland, 1919) that the variability in height of sunflower plants was a minimum at the end of the first week, increased during the next three weeks, and subsequently was fairly constant in variability. The coefficient of variation of maize (Pearl and Surface, 1915) and of apricot trees (table 4) was largest in the young plants and decreased with age. The number of veins in beech leaves (Pearson and Radford, 1904) was more variable in the first formed leaves on a spray than on those subsequently formed. The variability of the early nepionic leaves on *Sium cicutaefolium* decreased in successive leaves (Shull, 1905).

Records of the yields of fruits in consecutive years, while scanty, afford a larger basis for comparison. Orange trees (Batchelor and Reed, 1918) and apple trees (Hedrick, 1911) showed no more variability in yield over a period of six or seven years than for any particular year in the period. The probable errors of yields of black currants (Hatton, 1925) showed a great drop from the first year of bearing to the second, but no significant changes thereafter.

3. *The relation between the size of a shoot and that of the organ from which it grew*

It is believed that there is a relationship between the size of a vegetative organ and that of the stem on which it developed, but the problem is one which has not been quantitatively studied with the thoroughness which its importance seems to require. If we regard any particular organ as a parasite on its mother shoot, its size would depend to a large extent upon the supply and rate of

transfer of necessary materials to the young organ. If, however, we regard the relationship as one of commensalism, then it is clear that the only way in which one can determine the relations is by investigation of actual cases.

In the case of larger plants there is a difficulty confronting the investigator at the outset due to the fact that a stem produces a varying number of branches and that their size depends to a large extent upon their age as well as upon other factors.

The production of primary laterals on branches of the apricot tree does not indicate a high degree of relationship between the length of the branch and the total number of laterals it bore in the first year (Reed, 1924). If we adopt the following designations we may state the results in the form of coefficients of correlation:

a = number of laterals per branch
b = total length of laterals per branch
c = length of branch

The following coefficients of correlation were found,

$$r_{ac} = 0.337 \pm 0.067$$

and

$$_{b}r_{ac} = -0.313 \pm 0.013$$

which means that, if all the laterals were the same length, there would be a negative association between the length of branch and number of laterals produced.

The relation between the length of the branch and the length of the laterals it produced is, however, more to the point and we may note the correspondence between the two characters:

$$r_{bc} = 0.700 \pm 0.040$$

Since the number of laterals on branches was itself a variable it is better to take the coefficient of partial correlation which expresses the correlation in case each branch had the same number of laterals

$$_{a}r_{bc} = 0.665 \pm 0.042$$

The comparatively large value of this coefficient shows that the longer branches of the apricot tree tended very definitely to have longer laterals.

The problem of organ size in bean plants has been carefully studied by Sinnott (1921) with respect to the dry weight of leaf, pod, and seed. A part of the determinations were made on immature plants, but the majority of the measurements were upon plants at maturity. From his paper a few data may be quoted:

Dry weight of shoot : Average dry weight of leaf, $r = 0.769 \pm 0.015$
Number of leaves: Average dry weight of leaf, $r = 0.607 \pm 0.023$
Dry weight of shoot: Average dry weight of pod, $r = 0.301 \pm 0.033$
Total weight of fruit : Average dry weight of pod, $r = 0.460 \pm 0.029$
Dry weight of shoot : Average dry weight of seed, $r = 0.229 \pm 0.035$
Total weight of fruit : Average dry weight of seed, $r = 0.390 \pm 0.031$

The coefficients represent what might be regarded as a significant degree of correlation but upon more careful consideration of the original data one can hardly draw that conclusion. Sinnott skillfully showed that there is an increase in organ size with increasing body size up to a certain point only, and that beyond this point an increase in the size of the plant is not accompanied by an increase in the size of the leaf, pod or seed. His explanation of this relation is derived from the fact that the size of an organ is dependent, not on the size of the stem from which it arose but upon the size of the growing point; on this assumption the small plants are those which did not attain at maturity sufficient size to have

arrived at the maximum stem (growing point) diameter. In such plants a significant correlation might be expected. In the case of the larger plants, however, Sinnott suggests that there is no relation between body size and growing point size and consequently no correlation between body size and organ size.

The next problem was to investigate this possibility. It is of course difficult to measure the size of the growing point and the cross-sectional area of the stem is obviously unsuited for the purpose. Sinnott believes however that the cross-sectional area of the pith of the internode below the attachment of the organ is satisfactory for the purpose. He accordingly made measurements of leaf and pith area on twigs of *Acer saccharum*. The coefficient of correlation between the two characters was 0.807 ± 0.024 and the regression was linear, confirming the idea that the size of the plant organ is dependent, not upon the body size of the plant on which it is borne, but upon the size of the growing point from which it developed.

4. *The correlation between size of an organ and its position on the stem*

The shapes of plants which ultimately depend on the size and position of their parts are more or less characteristic. Casual observation is sufficient to distinguish a fir from an elm even at some little distance. Yet when it comes to a precise description of the arrangement of plant organs we seem to have little real quantitative information on the subject. A few decades ago the subject of phyllotaxis was quite extensively studied by those having leisure for such things, but we cannot see where their results contribute anything to the static or dynamic problems of growth as there was no concrete relationship obtained between size and position of leaf. It seems, however, that a study of the problem ought to be facilitated by an assumption that the pattern of the organism is the result of a process of growth and differentiation which is largely an expression of inherent factors.

We come to see a larger meaning in the words of Dutrochet (1822) "La tige d'un végétal quelconque, considérée dans son ensemble et abstraction faite des bourgeons adventifs, offriroit un aspect parfaitement régulier, si tous les bourgeons se développoient, si toutes les branches auxquelles ils donnent naissance prenoient un accroissement semblable ou proportionelle. Mais l'avortement d'un grande nombre de ces bourgeons, la différence de la nutrition, qui est active dans quelques branches et languissante dans quelques autres, amènent dans la tige du végétal une irrégularité qui n'étoit point originaire."

The functional relationships between the size of an organ and its position on the stem has received comparatively little study by botanists and even they have devoted attention to the seed-bearing rather than to the vegetative organs. The size of a leaf whorl (number of leaves) in *Ceratophyllum* was shown (Pearl, 1907) to increase in number from the proximal to the distal part of the plant in a way which was well expressed by the equation

$$y = A + C \log (x - \alpha)$$

"That is, the absolute size of the elements of the developing system given by a *Ceratophyllum* branch is modified by environmental differences, but the law which describes the proportionate differentiation of the elements is independent of the environmental history of the plant." This may be interpreted to mean that the size of any particular whorl of leaves is a

function (in the mathematical sense) of the number of whorls which have previously been formed on that axis. Pearl's work showed that the size of whorls on primary and secondary lateral branches also followed the same law of growth as those on the main stem.

Another relationship of importance was that of the variability in leaf-number of successive whorls. An extensive study of the coefficients of variability of leaf-number showed that the number of leaves on successive whorls were characterized by an ever increasing constancy to their type.

When the *Ceratophyllum* branches were studied with respect to their distribution on the stem, relations quite similar to the above were discovered. While the production of branches on the lower part of the stem was somewhat irregular so far as their location at nodes was concerned, their production became more regular as they approached the distal end of the stem.

The mean length of laterals on pear branches showed some tendency to fall on a curve of the form $y = a + bx - c \log x$ when y equals length of lateral and x represents the ordinal position of the lateral on the branch (Reed, 1921b).

The relations between position and length of fruiting branches of sea-island cotton (Mason, 1922) suggest a paraboloid curve but the author did not attempt to obtain an equation for it. This plant should yield profitable data for study because a fruiting branch is ultimately formed from the extra-axillary buds of every node of the central axis.

The problem of the distribution and the length of apricot shoots on the stem axis was briefly studied by the writer (Reed, 1924a). Casual observation of an apricot branch shows that primary laterals occurred in three fairly well defined groups. The laterals occupying the center of a group were those of maximum length, from which their length gradually decreased. The group of laterals nearest the proximal end of the branch was the largest and produced the longest laterals. The second group consisted of fewer and shorter laterals than the first, and was separated from it by an average of 20 nodes which remained dormant. The third group of laterals was not so well defined as the others, but showed many of the same features.

The symmetrical arrangement of the laterals in each group is a feature which suggested that their lengths conformed to a logarithmic curve.

When the scale of mean lateral length for each branch was arranged so that the center of group I fell on node 48, the three symmetrically shaped groups of laterals were easily distinguishable.

If we assume that the cyclic growth of the laterals was in some way similar to the cyclic growth of the branches which bore them, the summations of their length, beginning at the base of the branch should give a curve resembling that of growth. It was actually found that their values agreed closely with an equation of the general form

$$\log \frac{y}{a - y} = K\,(x - x_1)$$

where y = length of lateral grown from node x; x_1 = the node at which y had attained half the length of a for the cycle; a = the maximum, or limiting, value of y; and K = a constant.

If the lengths of the individual laterals be regarded as increments in the length of a system, then the differential form of the above equation ought to express their lengths for each nodal position.

$$Z = \frac{dy}{dx} = ky\,(a - y)$$

here $\quad k = K/A$

This was found actually to be the case and the calculated values were in good agreement with the observed. The three curves showed the decreasing amplitude characteristic of the groups of laterals on the main branch.

A brief discussion of the relation between rate of growth and structure has recently been given by Penrose (1925). When each new part arising on a straight axis possesses growth properties similar in certain respects to those possessed by the apical group of cells, repeating structures are formed, e.g. fronds of the Male Fern or leaves of Fool's Parsley. In these instances the ability of the part to repeat the structure of the whole is expressed in three stages, the last being incomplete. More commonly the repetition in shape is limited to one stage, because the parts are not themselves similar in shape to the whole, but only to one another, though the size of the part bears a constant ratio to that of the whole plant. The dimensions of successive members form, in such a case, a geometrical progression, provided the system of growth is uniform.

Penrose gives examples to show that the sizes of successive leaves and of their internodes give values which closely approximate the curve of autocatalysis. The equation to the curve of outline of the plant structure is

$$x = A(1 - e^{-L/A})$$

Here x = the length of vein, leaflet, or internode; L = length of axis; A = the limiting or maximum value of x; and e = base of the natural logarithms. Obviously, this is the equation to a logarithmic curve.

The gradient in the growth capacity of homologous parts along an axis must be recognized. The leaves on certain parts of a stem are always smaller than those on the middle region. His data constitute further evidence of the usefulness of the autocatalytic curve in studying growth.

5. *The length and frequency distribution of laterals on the branch in relation to the problem of growth and differentiation*

In water one finds many plants showing a symmetrical development, indeed it is the best medium for the growth of simply organized plants. But the plants which live in a fluctuating environment are not usually symmetrical except in a very restricted way. It is possible that the universal tendency for development meets opposition of a kind that acts to bring about differentiation in an environment which is often sub-optimal.

There is recent evidence that the accumulation of metabolic products has a marked influence on growth and differentiation. The place at which they accumulate and the rate of transformation, may therefore play a part in differentiation.

The total output of differentiated material as measured by the length of lateral branches on a shoot tends toward uniformity (Reed, 1921b, 1924a). There is variability, of course, but no more than one finds in the lengths of the mother shoots themselves. The total lengths of laterals of pear shoots in the first year showed a root-mean-square deviation of less than 10 per cent of the mean. The resulting branch-patterns range from a system composed of few but long laterals to one composed of many, but short, laterals.

We may consider the length of the laterals on a branch, since this phase of differentiation is one which influences the pattern of the plant. The longest laterals are not necessarily the oldest, nor those at the extremity of the mother shoot.

The branches of fruit trees produce many more short laterals than long. When

histograms representing the distribution of length are drawn, they show an unsymmetrical distribution about the mean due to the higher frequencies in the lower classes. The distribution of short laterals on many trees determines in large measure their capacity for producing fruit. The distribution of apricot laterals has a pronounced asymmetry due to the predominance of short laterals. The mean length of 2528 primary laterals had a coefficient of variability of 110.53 ± 1.95. Asymmetrical distributions were also found in *Ceratophyllum* (Pearl, 1907), short branches being produced with much greater frequency than long branches.

These facts taken together are good evidence that the length of shoots on a tree or plant is governed by some very definite factor so fixed in its action that the law of chance is practically eliminated.

The number of blossoms per branch has been but little studied with respect to distribution, yet it is an important subject in differentiation. The blossom is a highly energized center on the vegetative organs toward which some of the most important synthetic materials migrate from other parts of the tree. The formation of a sufficient number of viable fruit buds is one of the obvious factors of success in the struggle for existence on the part of a species.

A survey of young apricot branches at the end of their first season's growth showed that the frequency distribution was asymmetrical owing to the more frequent occurrence of few blossoms per branch. The coefficient of variability of the mean was 60.39 ± 4.28.

Most of the blossoms were borne on the primary and secondary laterals of the apricot branch and there is naturally a relationship between fewer blossoms and shorter laterals, both of which have been shown to predominate on this tree. The ratio of blossoms on primary and secondary laterals of group I (the oldest group) was approximately 3:2, therefore the age factor does not seem to be the determinant for blossom-bud formation. The coefficient of correlation between the number of blossoms per branch and the ratio of primary laterals to total number of nodes per branch was

$$r = 0.386 \pm 0.065$$

The coefficient is positive and indicates that factors which cause the formation of numerous laterals also tend to form a larger number of flower buds. Of course the situation is more complex than this sounds, for example, the increased amount of photosynthates produced due to an increase in primary laterals would probably increase the formation of flower buds. Again it is possible that the formation of the two kinds of units (laterals and flower buds) is an expression of the same tendency to differentiation on the part of the tree.

Another step in the study of the problem consists in attempting to learn what relation there is between the length of a lateral and the number of blossoms it can produce. There is an opinion current that short laterals bear a proportionally larger number of blossoms, but the impression may be due to the fact that the blossoms on them must of necessity be closer together and hence more conspicuous.

In the paper cited (Reed, 1924a) the coefficients of correlation were determined with interesting results. If

a' = number of blossoms on primary laterals

b' = number of nodes on primary laterals

c' = length of primary laterals

the coefficients of gross correlation are

$$r_{a'b'} = 0.089 \pm 0.020$$
$$r_{a'c'} = 0.077 \pm 0.020$$
$$r_{b'c'} = 0.969 \pm 0.014$$

and the coefficient of partial correlation is

$$r_{a'b'.c'} = 0.059 \pm 0.021$$

This coefficient shows plainly that there is no correlation between the number of blossoms and the number of nodes on a lateral.

Similarly for secondary laterals

$$r_{a''b''} = 0.118 \pm 0.018$$
$$r_{a''c''} = 0.122 \pm 0.018$$
$$r_{b''c''} = 0.971 \pm 0.001$$

and

$$r_{a''b''.c''} = -0.002 \pm 0.018$$

Here there is no correlation between the numbers of blossoms and nodes upon the secondary laterals.

The frequency surfaces showing the association between nodes and blossoms brought out some important relations. They showed that in each case there were two rather well defined groups of laterals, (a) a large number of fruiting laterals and (b) a smaller number of distinctively vegetative laterals on which relatively few blossoms were produced. They also showed the essentially asymmetrical types of distribution in the two cases.

The relation between the position of a lateral and the number of blossoms it bore was also investigated, in order to see whether the lower (proximal) laterals produced more or less blossoms than the upper (distal) laterals on the branch. The coefficient of correlation in this case was

$$r = -0.109 \pm 0.022$$

This small degree of negative correlation may be interpreted to mean that the lower laterals were only slightly, if at all, superior to the others in the production of blossoms. These results indicate that the laterals of the apricot tree tend toward remarkable uniformity in the production of blossom buds.

Mason (1922) has briefly discussed this tendency for sea-island cotton plants to produce increasingly uniform numbers of nodes on fruiting branches. The coefficients of correlation were all positive and their values were greater for apical than for basal zones of the fruiting branches. "This was considered to indicate the presence of some factor which tended to limit the development of all fruiting branches, and that its influence became more marked as development proceeded." The removal of vegetative branches had a tendency to decrease the coefficients of correlation and suggested the introduction of an additional factor which definitely inhibited the development of the fruiting branches in the unpruned plants. Mason presented a hypothesis that this is due to the deflection of growth-promoting substances from the central axis system as a result of the unrestricted growth of the vegetative branches, and that the senescence of the central axis system is likewise ascribable to the deflection of these substances to the basal fruiting branches.

The effect of position upon the size of seed has been little studied. Harris (1915) found, however, some correlations between position and size of bean seeds which show a small, though positive correlation. This would mean that the weight of a seed is greater as the distance from the base of the pod increases. He has also shown (Harris, 1917) the existence of a negative relationship between bilateral asymmetry and the capacity of beans for maturing their ovules into seeds, that is, asymmetrical pods were less capable of seed development than symmetrical pods.

6. Age and size of vein islets

There have been investigations which produced evidence that the size of vein "islets" tends to decrease with age of the individual. The problem is rather difficult because of the inherent variability of the material and other investigators have come to the conclusion that there is no difference in the size of the so-called islets. We must therefore conclude that the question is still open.

7. Age and teratology

The proportion of teratological fruits in *Passiflora* was found (Harris and Gortner, 1914) to be a maximum among those first formed and to decrease as the plants became older.

On *a priori* grounds it might be expected that the tendency to produce abnormalities had some relation to the age of the individual, whether this consisted in the "wild oats" type of abnormalities due to the vigor of a young plant, or in the doddering imperfections of the senile period. The question is one of enormous importance in the evolution of a type or species, yet I find but few studies on it. It is a subject in which there is need of rigorous definition and exactness to avoid needless, not to say trivial, work.

IV. DIFFERENTIATION AND DEVELOPMENT

There is at present a hiatus in our ideas of the causal relationships between form and physiological forces, due perhaps to the fact that the chemical physiologist is less accurate in his analytical studies of the plastic shoot-forming substances than the biometrician who measures the products of the growth process. There must be a series of causal factors which bring about the more or less constant results in the form of individuals of this or that species of organisms. It will not suffice merely to weigh, measure, and correlate the organism unless we are content with a very limited view of the growth process. Most forms of life (except the most primitive) are characterized by an axial structure. Organisms living in a comparatively constant *milieu* have a relatively symmetrical structure. In a fluctuating *milieu* the untoward conditions are met by differentiation which leads to the production of an organism which lives on and produces offspring under conditions which would otherwise be prohibitive. The present state of our knowledge leads us to believe that much of the energy expended by the plant during growth goes to maintain an equilibrium between the organism and its environment which is favorable to the processes of development. A part of this energy may well be expended on differentiation.

1. The problem of dominance of the apical meristem

The axial structure which characterizes the higher forms of life results from a more rapid rate of growth in one direction than in others. The simple manner of growth of the filamentous thallophytes gives way to the many angled development due to localized meristems of root apices and of apical buds seen in the spermatophytes. The dominance of these meristematic regions impresses the casual observer, and since it is one of the most fundamental aspects of differentiation in plants we shall discuss recent studies on its action. Many of the statements found in the discussion of the question of apical dominance are vague and others are mystifying. The statement that "the available food materials of the stem are principally devoted to the development of the apical bud" raises more questions than it answers. The statement that the

growth on an upright branch is regulated by "polarity" falls into the same category. In the sense that polarity has been applied to the formation of shoots and roots upon cuttings, this idea would be inapplicable to the factors determining shoot or flower formation, since, in its implication, polarity involves the idea of two mutually exclusive qualities—for example, the opposite ends of a magnetized bar of iron. The idea of an "axial gradient" is a more exact designation of the phenomenon but does not account for the production of the gradient.

In recent years there has been a vital interest in this problem and we may discuss some of the investigations which have dealt with it.

Loeb (1916) explained the results of his experiments with *Bryophyllum* in the sense of Sach's theory of the upward flow of shoot-forming substances and the downward flow of root-forming substances which determine when and where dormant buds shall begin to grow. In his later work he advanced the idea of an inhibiting substance which was supposed to arise in the apical region and to move toward the subapical buds, keeping them in a dormant condition, while the apical buds were thereby freed from this substance and capable of growth. Subsequently he renounced this idea and believed that the inhibiting action of one part of the plant upon another is due to the fact that the sap begins to flow to the *anlagen* which first begin to grow, and that the other parts remain dormant because of the continuous flow of sap to the most active *anlagen*.

This idea of the effect of the flow of foodstuffs in producing polarity is seen in the writings of others. Curtis (1920) who is one of its most successful advocates has succeeded in destroying apical dominance in cuttings by injecting them with solutions of sucrose and other substances.

No more perspicacious views have been advanced than those of Robertson (1923) in ascribing the growth reaction in regenerating organisms to an autocatalyst which is produced in the cell nucleus and escapes into the pericellular fluid during mitosis. Cell division is regulated by the relative volumes of nucleus and cytoplasm (the nuclear-cytoplasmic ratio). Every cell then contains endogenous autocatalyst in the nucleus and exogenous autocatalyst in the pericellular fluid. Under conditions of equilibrium the sum of the amounts of endogenous and exogenous autocatalysts is a constant; if the endogenous supply is large then the exogenous supply is small, and vice versa. Hence if the supply of exogenous catalyst is large only a small supply of endogenous autocatalyst can be produced before equilibrium is imposed upon the reaction. Thus the substance produced by any part which is capable of influencing regeneration in any other part, is one which inhibits the growth of the part in which it is produced.

"The nuclear autocatalyst therefore combines in itself all the properties necessary to bring about the effects observed by Loeb, and we have furthermore merely to assume the existence of varying degrees of differentiation in the cells composing the fragment of stem to understand how one and the same substance, namely, the nuclear autocatalyst, may inhibit the multiplication of one type of cell while actually promoting the multiplication of another" (p. 211).

Studies on the process of growth in cuttings and in amputated shoots at this laboratory have yielded no little information upon the problem of uni-directional growth, or polarity.

Unusually strong dominance exists in

the apical regions of shoots of the pear tree (Reed and Halma, 1919). So long as the apical bud of a shoot grows uninterruptedly there is seldom any development of lateral shoots. If, from any cause, the apical bud of a shoot is arrested in its development, a neighboring lateral bud promptly develops and the shoot from it continues the axial growth.

If the apical portion of a shoot be amputated at the end of the growing season, as in the process of "heading back," several lateral shoots arise from buds directly back of the point of amputation and the most distal bud not only is the first to grow but also invariably produces the largest growth.

The lateral shoots which develop in such a case are progressively smaller as their distance from the apex increases. In a case already mentioned their lengths were expressed by the equation

$$y = 93.47 + 4.193\,x - 136.907 \log x$$

where y = length of lateral shoot and x represents its ordinal position (counted from the apex) on the parent shoot. These facts lead one to conclude that growth is influenced by some factor which is unequally distributed in the shoot.

2. Factors controlling dominance

This dominance of the apical region of the stems of Chinese lemon is so pronounced and characteristic that one can only conclude that it is due to some significant internal factor. Experiments were planned for the purpose of getting information upon the nature of the agent which instigated this apical dominance.

When cuttings of Chinese lemon shoots are suspended vertically in a moist atmosphere, shoots develop from buds at the apex of the cuttings and roots (usually from the callus) at the basal end. This occurs whether the cuttings are in the normal or inverted position. The cuttings will live and continue to grow for several months, but shoots develop only from two or three buds nearest the apical end of the cutting. If these buds are killed by burning them with hot glass rods, or gouged out, the buds next below them will develop, but if the apical buds remain functional and develop, the lower buds remain dormant. If the sprout from an apical bud be removed after having reached a length of a few centimeters, a new sprout will develop from one of the accessory buds but the lower buds remain dormant as before. If the tip of a sprout be removed, growth will continue from one of the lateral buds of the sprout, but the sub-apical lateral buds on the cutting remain dormant. Young shoots on the trees remain in an unbranched condition unless the tips are cut off.

The course of events may be followed somewhat more accurately when the growth of buds is inhibited by encasing them with material which mechanically prevents growth and which may be removed at any time. In our first experiments we encased the upper part of cuttings in a thick cast of plaster of Paris which prevented the development of the buds it covered. A few weeks later sprouts appeared from buds situated just below the plaster cast, as though they were apical buds. After the sprouts on each cutting in the experiment had reached a length of several centimeters, the plaster casts were removed and the cuttings suspended again in the moist chamber. In a very short time the buds at the apices of the cuttings began to grow out and sprouts were formed in the typical manner. As they grew the sprouts produced near the middle while the cutting was enclosed in plaster of Paris ceased growing and eventually some of them died, but the sprouts from the apical buds grew normally.

The quantitative relations of the effect of this sort of treatment have been studied in detail by Halma (1926) using Chinese lemon cuttings which were tightly wrapped with strong rubberized tape. Each cutting possessed ten buds. In one lot of cuttings the three distal buds were wrapped, in the second lot the five distal buds were wrapped, and in the third lot none were wrapped. The length of sprouts on each cutting was measured every few days. At intervals the tape was removed and record was made not only of the length of sprouts at that time, but of both subapical and apical sprouts at the end of the experiment. Growth started from buds on the unwrapped part of these cuttings only a few days later than from the apical buds of the unwrapped cuttings. After removing the wrappings none of the subapical sprouts died.

The growth of sprouts on both the wrapped and unwrapped portions of the cuttings follows the course of an S-shaped curve, suggesting the possibility that the two portions, although connected morphologically yet behave as separate physiological units. Upon further measurements of growth and variability of the material Halma concluded that they were physiologically distinct units. The same tendency toward apical dominance was manifested by each portion of the cutting. In 30 per cent of the cuttings whose upper three buds were wrapped the third bud remained dormant after the tape was removed. In the case of cuttings whose five uppermost buds were wrapped only 6 per cent produced sprouts from all five buds after the tape was unwrapped. As a rule only the first, second, and third buds developed, where five buds had been wrapped.

Halma cogently discusses the bearing of these facts upon the nature of regeneration in stems. "There is no doubt that the growth of the cuttings under the conditions of the experiment depends upon the material stored in the stem, and that this supply becomes exhausted regardless of the number or position of the sprouts produced. According to Loeb the sprout, or sprouts, which grow out first attract all the available material, hence the other buds remain dormant. The above investigation shows clearly that this is not true for Chinese lemon cuttings, because in many cases the sprouts below the inhibited portion were of considerable length before the tape was removed and yet growth was not prevented in the apical region.

The interpretation of the results of earlier experiments was based on the assumption that an inhibitory substance, produced by the growing apical sprouts, passed toward the basal part of the cutting and thus inhibited the development of sprouts in that region.

From this experiment, it is obvious that that assumption was inadequate, because in this case the apical region of the cuttings had no sprouts to produce an inhibitory substance and, furthermore, when apical sprouts were produced, these were unable to suppress the growth of subapical sprouts.

If we assume that dominance is due to an axial gradient of metabolism declining steadily with the distance from the apex, then a lemon shoot ought to produce a gradation of sprouts from apex to base. This gradation, however, appears only in a part of the shoot. Furthermore, less growth ought to be produced in the subapical than in the apical region. This was not the case with taped cuttings, where both the upper and lower portions produced growth in proportion to their mass. There is also no consistent difference in the amount of sprouts produced by the different parts of the mother shoots.

A possible explanation of these experiments is based upon the view held by

Curtis (1920) that some substance necessary for growth passes upward through the phloem. On this assumption, in the control cuttings the growth promoting substance would move upward until it reaches the uppermost bud or buds which are in condition to make use of it.

But cuttings planted upside down also produce sprouts from the apex, hence we cannot say that this substance can only move upward. We have seen that in the free portion of the taped cuttings sprout growth started later than in the apical portion of the control cuttings. This time factor is significant. We may assume that the transformation of food reserves into growth-promoting substances is a gradual process which begins at the apex. This view is strengthened by the fact that when only the three uppermost buds were inhibited, the delay in the outgrowth of buds immediately below the tape was not as great as when the five uppermost buds were inhibited.

No definite reason can be given as to why the transformation of food reserves into growth-promoting substances should begin at the apex. Evidently it takes place just as quickly in taped as in untaped cuttings for sprouts will break through weak places in the tape before there is any sign of growth below the tape.

The results obtained warrant the assumption that the earlier release from dormancy of the buds in the apical region is due to the gradual transformation of food reserves into growth-promoting substances from apex to base. The dormancy of sub-apical buds may be assumed to be due to the ability of the actively growing apical sprouts to draw on the entire supply of growth-promoting substances as fast as they are formed. If the growth of apical sprouts were dependent upon the supply of these substances which are present in that region only, then buds all along the cutting would have to grow out in order to account for the mass relation obtained.

It was also shown that the growing sprouts below the taped portion cannot draw on the supply of growth-promoting substances which are stored up in the apical part.

It seems to the writer that the above explanation is more plausible than that based on the downward flow of some inhibitor. A recent investigation by Gardner (1925) also indicates that nutritive factors are involved in the initiation of sprout growth."

Halma has discussed at some length the intraseasonal cycles of growth produced by lemon trees in their relation to the growth of sprouts. During the first period growth probably is produced at the expense of stored material, later it depends on materials manufactured contemporaneously. (Gardner (1925) has noted that starch disappears first from the apical part of a shoot as the spring growth begins and progressively disappears downward.) The transformation of food reserves into growth-promoting substances during the first period of growth in lemon trees begins probably at the apex and the supply is appropriated by the growing sprouts as fast as it is formed, hence the basal buds remain dormant. Since the subapical sprouts on the wrapped shoots were later in developing than apical sprouts on unwrapped shoots it seems reasonable to assume that the former can draw upon the supply of growth-promoting substance only when it lies below the point of origin of the sprout.

During the second period growth is confined to a few apical sprouts under favorable conditions. The amount of raw materials furnished each shoot depends upon the supply and the competition among different organs. We must seek an explanation for the fact that the upper-

most sprouts on a shoot grow so largely at the expense of those below them, i.e., for the continuance of polarity. No better explanation appears than that the rapidly growing apical sprouts exert an inhibiting influence upon the growth of those situated below them. This influence, as Loeb (1917) suggested, may be due to an actual substance (a chalone) which is produced in the growing tip and, passing toward the base, prevents further elongation of subapical sprouts. The inhibiting substance does not depress growth in the apical sprouts because ordinarily it is carried away as fast as it is formed.

These assumptions are well sustained by the results of numerous experiments which Halma performed on horizontal cuttings and shoots. When cuttings or unbranched shoots are placed horizontally, sprout development is confined to the dorsal side of the shoot except for one or two sprouts which develop on the ventral side near the apex of the shoot.

The results of several experiments go to show that this asymmetrical type of growth is due to the distribution of some growth-controlling factor and not to inherent differences in the constitution of the shoot. If all buds on the dorsal side were destroyed none of the buds on the ventral side developed into sprouts though adventitious buds on the dorsal side produced sprouts. For three consecutive years all sprouts on the dorsal side of horizontal shoots were rubbed off as fast as they developed yet none of the buds on the ventral side, with the exception of one or two near the apex, showed any sign of growth. When a horizontal cutting is allowed to develop sprouts from the dorsal side and is then rotated through an arc of 180 degrees, the buds from the previously ventral side then produce sprouts, while the original sprouts gradually cease growth and, in some cases, die.

When buds on the ventral side of a horizontal shoot were given a certain degree of isolation 73 per cent developed sprouts. The isolation was given by making a slanting cut, beginning about one centimeter on the distal side of the bud and extending into the wood to a point one centimeter on the proximal side of the bud. This severed the bud from the mother shoot except on the proximal side. A small plate of mica was inserted in the cleft to prevent the wound from healing. If the cut were made in the opposite direction, leaving the bud area attached on the distal side, none of the buds produced sprouts.

Quantitative studies on the growth of sprouts on horizontal shoots led to some satisfactory conclusions, and throw some light on the rôle of shoot forming substances in the formation of sprout growth. A lot of unbranched lemon shoots were bent and tied in a horizontal position before growth started in the spring. Half of the shoots were kept in this position during the entire season and the others were bent in the opposite direction when their sprouts had an average length of 5.4 cm. In less than two weeks the buds which were previously on the ventral side began to develop sprouts and although the growth of those now on the lower side was not suppressed, the growth of those on the dorsal side exceeded the others by a few centimeters in length when growth ceased for the season.

The evidence from the behavior of horizontal shoots goes to support many of the foregoing ideas of the factors which influence growth and differentiation. It appears that growing sprouts on the dorsal side are able to draw on the supply of growth-promoting substances which are contained in the dorsal as well as the ventral side of the shoot. Therefore, the growth on horizontal shoots was approximately equivalent to that produced on those reflexed

shoots which produced two sets of laterals. The longitudinal movement of growth promoting substances is slight because a notch below a bud on the ventral side prevents growth-promoting substances from reaching it, while a notch on the distal side permits it to grow but affects only that one bud. After the stored food reserves are utilized, notching on the distal side of buds on the ventral side is not effective in starting sprout growth from them. Therefore the initial period of sprout growth is evidently dependent on this accumulation of starch and other reserve material. We can hardly assume that the production of an inhibiting substance by the sprouts on the dorsal side prevents buds on the ventral side from developing because when all dorsal sprouts were rubbed off for three years no growth came from buds on the ventral side of the shoots. Furthermore, when sprout-bearing shoots were reflexed, a new set of sprouts grew from buds which had previously been ventral and the new set of sprouts showed no retarding effect on the original sprout until the end of the first growth cycle.

The appearance of sprouts on shoots which have been bent into a horizontal position is not to be explained easily. The result has been ascribed by some to the compression of tissues and consequent impediment to the flow of sap to buds on the ventral side of the shoot. The incorrectness of this view has been shown by experiments (Halma, 1926) with young lemon trees grown in pots. Their shoots were bent at right angles to the axis of the plant and tied in that position. One plant was inverted so that the compressed tissues were on the dorsal side and the other remaining in the normal position suffered compression on the ventral side. In both cases growth occurred only on the dorsal side of the shoot.

When sprouts appear on the first few nodes back of (basad to) the bend the evidence is more in favor of the view that there is an obstruction to the passage of nutrient substance (Gardner, 1925), because in one case they may be on the vertical and in another on the horizontal part of the shoot.

The idea of an obstruction to the upward flow of growth-promoting substances has also been used in attempting to explain the development of buds in cases where notches or girdles have been cut just above them. There are many obstacles to the acceptance of this idea, however. It is more probable that *physiological activity* and not *accumulation* is the condition which initiates growth. The apical part of a cutting is normally the most active region physiologically, but it is possible by artificial means to raise the physiological activity of another region to such an extent as to make it dominant so far as shoot production is concerned. Jones (1925) found that a difference of no more than 2°C. was amply sufficient to convert a warmed into a dominant region, irrespective of its position in relation to the apical end of the cutting. When whole cuttings of seakale (*Crambe maritima*) roots were thus treated shoots could be induced to arise from the root-apex end if a higher temperature was maintained at this end of the cutting. "It seems legitimate to conclude from these experiments that whilst the whole of the cambium has potentiality for bud production, this gains expression chiefly in regions where the cambium is exposed and physiologically most active."

3. *The metabolic gradient*

There is yet to discuss the theory of the "metabolic gradient" which has been formulated by Child (1915). Although it adds little to our understanding of the causes which determine differentiation in the plant, it is an admirable statement of

the problem and gives us a convenient framework upon which to arrange our ideas. It emphasizes the kinetic aspect of the problem by relating the differentiating processes to increased or decreased metabolic activity. The problem of differentiation is not so much a question of the presence of organs as of their position and relative size. It seems to me that the solution of this problem must in large measure depend upon activity and less on the Sachsian concept of shoot- or root-forming substances. Child considers that the intensity of metabolism, measured by intensity of respiration or response to stimuli, shows a definite variation in different parts of the organism, indeed in a single organ, and that these gradients determine the fundamental outlines of axial symmetry and structural differentiation. Centers of high metabolic activity like the head of a planarian worm or the apex of a stem tend to dominate centers of lower metabolic activity. Gradients may be reversed or obliterated, or new gradients established by environmental conditions which modify the metabolic rate in different parts of the organism, but the gradient once established, persists through asexual and perhaps through sexual reproduction.

It is difficult to conceive that every possible activity of the organism is dependent upon a gradient of substances appropriate thereto. One soon has the plant full to overflowing. But to consider that the gradients may represent gradual changes in the nuclear cytoplasmic ratio governing the activity of the autocatalyst may clarify our ideas on the subject.

V. CONCLUDING DISCUSSION

The foregoing subjects have been discussed with the hope of clarifying our understanding of the problem of growth and differentiation in plants. If this incomplete treatment has any merit it consists in directing the attention to recent work on the problem, and to the importance of quantitative studies in this field.

Growth is a complex process, yet it is surprising that the application of a few simple mathematical operations should throw so much light upon its nature. If the discussion has erred on the side of over-simplification, it is because it seemed best to lay aside all irrelevant matters and discuss growth as a slow transformation of material at a rate proportional to time. This ought to emphasize the fact that the forms and functions of organisms, though variable, nevertheless are not outside the realm of exact science. Much additional work is needed to discover the quantitative relationships governing the so-called pattern of organisms. It seems reasonable to expect that the position as well as the size of organs bears a definite correlation with certain properties (morphological or physiological) of the other parts of the organism. The examples discussed here and elsewhere, justify the expectation that an extension of quantitative work will do much to obtain that orderly, verifiable mass of knowledge which can truly be termed *science*.

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DIFFERENTIAL FERTILITY

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THE PROBLEM

THERE has been a great dearth of adequate data from which to determine the relative degree to which the different social and economic classes of any human population reproduce themselves. This is particularly true for the population of the United States. At the same time the problem is clearly one of first class importance both theoretically and practically. It is the reproductive activity of the persons now living which determines the constitution of the population of the next generation to an overwhelming degree. Especially is this true in any country where there is naturally, or by legislative restriction, a limited immigration.

The pioneer attempt at an adequate statistical approach to the problem of differential fertility amongst the several social classes in a human population was that of Heron (1906). Using the correlational calculus he reached the following conclusions:

> As far as the present investigation goes it demonstrates I think conclusively that for the London districts there is a very close relationship between undesirable social status and a high birth-rate. In districts where there is overcrowding, where there is a superabundance of the lowest type of labour, where it is needful to employ many young children in order to earn daily bread for the family, where infantile mortality is greatest, there the wives of reproductive ages have most children. Where there is more culture and education as shewn by a higher proportion of professional men, where there is more leisure and comfort as shown by a higher percentage of domestic servants, where the traders who appeal to the improvident and thriftless are fewer in number, there the birth-rate is least. Again, where there is more general pauperism, where signs of bad environment like phthisis are prevalent, where pauper lunatics are most plentiful, there the birth-rate is highest. Cancer alone of the undesirable physical conditions dealt with so far seems more prevalent in the prosperous and cultured districts and to be associated with a lower birth-rate.
>
> Nor is the higher birth-rate of the undesirable elements compensated by the higher death-rate. The net fertility of the lower status remains higher than that of the superior status.
>
> The relationship between inferior status and high birth-rate has practically doubled during the last fifty years, and it is clear that in London at least the reduction in the size of families has begun at the wrong end of the social scale and is increasing in the wrong way. I have brought forward evidence enough to shew that the birth-rate of the abler and more capable stocks is decreasing relatively to the mentally and physically feebler stocks.

Broadly speaking these conclusions have been confirmed by all subsequent students of the problem, and have become incorporated into the accepted body of present sociological doctrine. I shall make no attempt at an exhaustive list of the literature. The following citations sufficiently support the point, and will lead the inquiring reader into the further literature: Brown, Greenwood, and Wood, 1920; Cattell, 1915–17; Cobb, 1912; Crum, 1914; Darwin, 1922; Elderton *et al.*, 1913; Fürst and Lenz, 1926; Gini, 1926; Hart, 1924; Hewes, 1911; Hill, 1913; Holmes and Doud, 1918; Johnson and Stutzmann, 1915; Lenz, 1926; Marshall, 1913; Near-

ing, 1914; Onslow, 1913; Pearson, 1909, 1910; Popenoe, 1917; Phillips, 1926; Savorgnan, 1923; Schiller, 1926; Spiegelberg, 1924; Sprague, 1915; Terman, 1925; Weinberg, 1909; Whetham, 1909.

Holmes (1921) sums the case up in the following words (p. 140):

> The elements of the population that are of subnormal mentality exhibit at present the highest degree of fecundity. This is the general verdict of most students of the birth-rate of different classes of the population. The higher death-rate of the subnormals probably does not offset completely their greater fecundity. . . . The classes in the higher social strata . . . . in general have a birth rate which cannot fail to lead to extinction. This much is clearly indicated from a variety of sources, while the springs of our defective inheritance have shown no manifest signs of drying up.

There have appeared in recent years a considerable number of studies on the fertility of groups of college and university graduates. The results have been generally held to be alarming in greater or less degree. Such socially desirable folk are not reproducing at anything like the rate desired by the conscientious eugenist.

But college graduates almost certainly do not include quite all the socially desirable people in the world. What is needed before a final alarmed judgment is reached is a fairly representative cross-section of all the different sorts of people composing the population. Brown, Greenwood, and Wood (1920) end their careful and enlightening study with these words (p. 205):

> The sociological implications of these results are left for the discussion of others. Here the personal impression is recorded that the analysis of the sample of middle class families has led to no result incompatible with the conclusions drawn by Professor Karl Pearson and his collaborators from wider data of a different kind.
>
> Whether these results, or any results of wider analysis, suggesting that neglect of eugenic principia is leading to a steady deterioration of the race are likely to influence the reproductive habits of the educated classes or social legislation designed to modify those habits, is a question we need not attempt to answer.

Reading between these lines, and also reading their first conclusion (p. 205): "In the first place, it is plain that there is no essential difference between the fertilities of women who have and of women who have not received a university education. Such differences of effective fertility as appear can be fully explained by differences of age at marriage," there arises some conviction that these English authors would be in sympathetic agreement with the second sentence of the preceding paragraph.

SOME NEW DATA

In the last issued report on natality from the United States Census Bureau (Birth Statistics, 1923) there is a table (numbered 10, pp. 171–181) which makes available some new and welcome data regarding differential fertility in this country. Once more the student of human biology is deeply indebted to the wisdom and insight of Dr. William H. Davis, who so ably and intelligently directs the collection and tabulation of the vital statistics of the United States. It is my purpose now to discuss briefly certain aspects of this new material. A preliminary report of this study, in which I was aided by Dr. John Rice Miner, has been published elsewhere (Pearl, 1926).

The data apply to the United States birth registration area *exclusive* of Delaware, Maine, Massachusetts, New Hampshire, Rhode Island, and Indiana. That is, the figures include California, Connecticut, Illinois, Kansas, Kentucky, Maryland, Michigan, Minnesota, Mississippi, Montana, Nebraska, New Jersey, New York, North Carolina, Ohio, Oregon, Pennsylvania, South Carolina, Utah, Ver-

mont, Virginia, Washington, Wisconsin, and Wyoming.

The original table provides the following information: The births, number of children born, and living, and average number born and living, to mothers of 1923, by occupation and age of father. The occupations of the fathers are grouped into the following main classes, with a number of smaller sub-divisions in each main class:

1. Agriculture, forestry, and animal husbandry.
2. Extraction of minerals.
3. Manufacturing and mechanical industries.
4. Transportation.
5. Trade.
6. Public service (not elsewhere classified).
7. Professional service.
8. Domestic and personal service.
9. Clerical occupations.

When one considers carefully the subdivisions under these nine main heads the usual difficulty with official vital statistics is at once encountered. Economically and socially differentiated groups are included in some particular general class from the remainder of which they are, in these respects, sharply set apart, in reality. But it is reasonably obvious that economic and social factors and forces are among the most important elements in determining the biologically significant environment of human beings, as they exist here and now. Relative wealth virtually determines the character of the immediate physical environment in which men live. Furthermore, economic and social position are significantly correlated with the amount of physical labor which individuals perform, and this has been shown (Pearl, 1924) to be biologically important.

In view of these considerations it was deemed necessary to reconstitute the main occupational classes, as given in the original document cited, so that they might conform at least somewhat more closely to significant reality. The general plan followed in this reconstitution of the classes was to take out of classes 2, 3, 4, 5, and 6, all subgroups in which the persons composing the subgroup enjoyed a distinctly and obviously higher economic and social position than the average of the main class as a whole from which they were removed, and put them into a reconstituted class 7. This procedure involved the following transfers: Operators, officials, and managers from Class 2, Extraction of minerals; builders and building contractors, and managers, superintendents, manufacturers, and officials from Class 3, Manufacturing and mechanical industries; captains, masters, mates, and pilots, and officials and superintendents (steam and street railroads) from Class 4, Transportation; bankers, brokers, and money lenders, commercial travelers, insurance agents and officials, and real estate agents and officials from Class 5, Trade; and officials and inspectors (city and county), and officials and inspectors (state and United States) from Class 6, Public service.

These transferred sub-divisions were then all put with Class 7, Professional service, as originally constituted. This latter class, as reconstituted, then includes not only professional men in the strict sense but the capitalists, officials, and managers, whose economic and social status is more like that of the professions than the other classes, so far as it was possible to treat them separately. In some cases this was not possible, as in the class Retail and wholesale dealers. Importers and exporters, and many of the retail dealers would be of the same economic and social class as the occupations which have been included with Professional service, but a majority of the class are probably small shop-keepers, and it

was therefore thought best to leave them under Trade, on the ground that probably a smaller error would be involved in so doing than in adopting the alternative procedure.

The net upshot of this manipulation is to leave all the main occupational classes except 7 composed chiefly of laborers, more or less skilled, but still persons whose living depends upon the daily performance of more or less routine tasks, *in contrast to* the persons composing the reconstituted class 7, who, in the large, get their living rather more by the exercise of their wits than of their muscles.

In order that there may be no misunderstanding the names of the main occupation classes which have been altered by the above described procedure will be printed in *italic* type throughout the remainder of this paper. This typographical usage will serve to indicate that the statistics so printed are for the *reconstituted* classes, and not for the classes originally so named in the official report.

The next and final point of method to be considered before coming to the results is that of age. The desideration in all studies of fertility is, of course, the completed family. In the present case, as usual, this desideration cannot be precisely attained from the available data. General consideration of the problem, and careful examination of all the figures themselves as given in the original report, led finally to the decision to deal analytically with the data for fathers aged 45 and over. This procedure will probably give as close an approximation as it is possible to get, from these or similar records extracted from the official standard birth certificate of the United States, to the unknown average size of completed family for the different occupational classes. In the textual portion of the original report from which the data are taken is the following statement (p. 20): "Particular attention is called to the data for fathers aged 40 to 49 years as these on the whole probably represent completed families." It is only after very careful consideration that I have ventured, in the treatment of the material here, to depart from the implication of the statement quoted. That 40 is too low a limit seems to be indicated by the figures themselves. In a majority of cases in the detailed tables the average number of children ever born is higher in the age group 45–49 than in the group 40–44. Again the detailed figures indicate that the inclusion of fathers over 50 in the group does not sensibly alter the averages which would be obtained by dealing with the age period 45–49 alone.

FERTILITY BY OCCUPATIONS

Table 1 presents the first set of basic data which we shall need in the discussion.

Before discussing at all the results of this table, it is necessary to consider some of the important peculiarities of the data. In the first place, if the figures of column (d) could be regarded as representing exclusively completed families, which they almost but not quite can, they would still give an erroneous impression of the gross fertility of the several occupational classes, for the following simple reason. All the data in the table are derived from the experience of women who were mothers in 1923. That is to say, they were women who were fertile in that particular year. No other women are included. No sterile matings appear, and no matings of generally low fertility throughout the mated life, except the few in which the female chanced to have a baby in 1923. That there are very few of such low fertility matings included is evident if it is recalled that we are here dealing only with families in which the father

was 45 years of age or over in 1923. In general the vast bulk of men who engender a baby when they are 45 years old, or over that age, are probably persons whose whole marital history has been characterized by relatively high fertility, as compared with the rest of their same social class.

The net result is that the values in columns (d) and (e) of table 1 somewhat exaggerate the true average fertility of the whole population of the same age in tional classes, as given by these data, are not safely comparable. The only essential difficulty with the figures is that the universe of discourse which they encompass is a definitely limited one, and we cannot safely generalize beyond these bounds.

With these limitations in mind it is easily deduced that the mothers of children born in 1923 by fathers aged 45 years or over, on the basis of column (d) of table 1, had total average progenies up to

TABLE 1

Children born to mothers of 1923, by fathers aged 45 years or over, by occupation of father, in reconstituted general classes of occupations

OCCUPATION OF FATHER	TOTAL BIRTHS (a)	TOTAL NUMBER OF CHILDREN EVER BORN (b)	TOTAL NUMBER OF CHILDREN LIVING (c)	MEAN NUMBER OF CHILDREN EVER BORN (d)	MEAN NUMBER OF CHILDREN LIVING (e)	MEAN NUMBER OF CHILDREN DEAD (f)	PER CENT OF CHILDREN DEAD (g)
Agriculture, forestry and animal husbandry	41,825	289,140	251,833	6.91	6.02	0.89	12.9
Extraction of minerals	*4,117*	*32,677*	*26,609*	*7.94*	*6.46*	*1.48*	*18.6*
Manufacturing and mechanical industries	*32,875*	*216,996*	*179,601*	*6.60*	*5.46*	*1.14*	*17.3*
Transportation	*4,480*	*27,002*	*22,997*	*6.03*	*5.13*	*0.90*	*14.9*
Trade	*6,771*	*34,885*	*30,389*	*5.15*	*4.49*	*0.66*	*12.8*
Public service	*949*	*5,189*	*4,374*	*5.47*	*4.61*	*0.86*	*15.7*
Professional service	*5,828*	*24,386*	*21,672*	*4.18*	*3.72*	*0.46*	*11.0*
Domestic and personal service	2,424	12,820	10,799	5.29	4.46	0.83	15.7
Clerical occupations	1,677	7,149	6,296	4.26	3.75	0.51	12.0
Totals	100,946	650,244	554,570	6.44	5.49	0.95	14.8

the various occupational classes. The probable magnitude of this exaggeration will be discussed farther on. The figures represent the average size of family of a selected sample only of the total population in each class, *the basis of the selection being high and probably historically continued fertility*. This means that, in the best case, we can only discuss from these data relative and not absolute fertility values. I see no reason to suppose that the relative fertility of the most fertile portions of the populations in the several main occupa- and including the 1923 birth, which stood in relative positions according to the occupations of the fathers as shown in table 2. These relative sizes of average families are shown graphically in figure 1.

From these data it is seen, in the portion of the population here under discussion, that when the average size of family produced by a mother of 1923 in her total reproductive life up to that time, by a father who fell in the *Professional* class and was 45 years of age or over in 1923 is taken as 1.0, the average size of family

produced from the mothers of 1923 by fathers who fell in the occupational class *Extraction of minerals*, and similarly aged 45 years or over in 1923 was 1.9. In general it appears that the relative average size of family in the different occupational classes in the case where we are dealing throughout with the selected more fertile moiety of the population, is in good general accord with what we have learned to expect from earlier studies in England and other countries. The professional, capitalistic group exhibits the lowest average size of family, and the labor groups, whether in factories, farms, or mines, the highest.

But from a racial viewpoint the matter

TABLE 2

Relative average size of family

Professional service	*1.00*
Clerical occupations	1.02
Trade	*1.23*
Domestic and personal service	1.27
Public service	*1.31*
Transportation	*1.44*
Manufacturing and mechanical industries	*1.58*
Agriculture, forestry, and animal husbandry	1.65
Extraction of minerals	*1.90*

needs to be pushed farther. There are a great many more farmers, or factory laborers, for example, in the whole population of the Registration Area than there are professional men. Let us next examine this aspect of the matter with some care. Table 3 lists the main occupational classes (reconstituted) in the same order as does table 2. In table 3, column (a) gives the number of males in each class who were 45 years of age and over at the time of the census of 1920. These are reduced in column (b) to relative figures, taking the reconstituted *Professional service* class as 1.00. Column (c), headed "Number of more fertile families in group, 1923," is a repetition of column (a) of table 1. This, it will be recalled, gives the number of births to mothers of 1923 in that year, by fathers who were 45 years of age or over. As has already been pointed out, those families within each

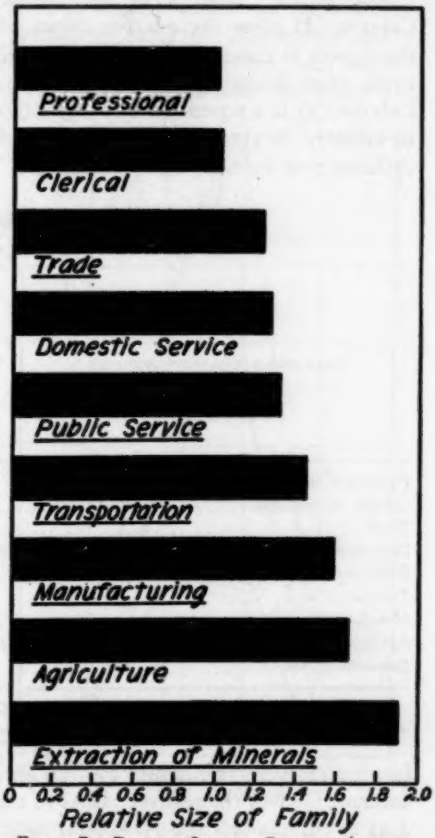

FIG. 1. BAR DIAGRAM SHOWING RELATIVE AVERAGE SIZE OF FAMILY EXPERIENCED BY MOTHERS OF 1923 IN THEIR REPRODUCTIVE LIVES UP TO THAT DATE, ACCORDING TO OCCUPATION OF FATHERS WHO WERE, IN 1923, 45 YEARS OF AGE OR OVER

occupational class, in which the wife had a baby in 1923 and in which the husband was at the time 45 years of age or over, represent on the whole the more fertile families in the group, taking the whole reproductive life together. Except

for small corrections, which ought to be made for multiple births and perhaps for illegitimate births, the number of births to these mothers and fathers, as given in column (c), gives the number of such "more fertile" families in the group. Column (d) gives the relative values of the figures in column (c), the *Professional service* class being again taken as 1.00. Column (e) is a repetition of column (b) of table 1. It gives the total number of children ever born in the "more fertile" families recorded in column (c). Finally, column (f) gives the relative values of the data in column (e), the *Professional service* class being taken as 1.00.

The relative figures of table 3, Columns (b), (d), and (f), are shown graphically in figure 2.

The results exhibited in table 3 and figure 2 are of a good deal of interest, and in some ways unexpected. Broadly what the figures show is that:

1. For each male 45 years or over in the class *Professional service* in 1920, there was 0.34 of a male of corresponding age in Clerical occupations; 1.00 in *Trade;* 0.47 in Domestic and personal service; 0.23 in *Public service;* and 0.79 in *Transportation.* In these six occupational classes more-fertile families, as defined above, occurred in about the same proportions relative to the *Professional service* class taken as 1.00 in both instances, as column (d) and the dash line of fig. 2 show. This means that in these six occupational groups more-fertile families are represented in about the same relative proportions to each other, as occupied males of corresponding age in the classes as a whole. This is only approximately true, because the figures of Column (a) are for 1920, and those for (c) for 1923. But the general consonance of the relative figures for the six classes named will probably not be significantly disturbed by this consideration.

2. For every male 45 or over engaged in *Professional service* in 1920, there were 3.22 workers of corresponding age in *Manu-*

TABLE 3

Absolute and relative figures for population and fertility

OCCUPATIONAL CLASS (RECONSTITUTED)	MALES AGED 45 AND OVER IN GROUP, 1920 (a)	RELATIVE PROPORTIONS OF ITEMS IN COLUMN (a) (b)	NUMBER OF MORE-FERTILE FAMILIES IN GROUP, 1923 (c)	RELATIVE PROPORTIONS OF ITEMS IN COLUMN (c) (d)	TOTAL NUMBER OF CHILDREN EVER BORN TO FAMILIES IN COLUMN (c) (e)	RELATIVE PROPORTIONS OF ITEMS IN COLUMN (e) (f)
Professional service	*624,180*	*1.00*	*5,828*	*1.00*	*24,386*	*1.00*
Clerical occupations	215,188	0.34	1,677	0.29	7,149	0.29
Trade	*626,321*	*1.00*	*6,771*	*1.16*	*34,885*	*1.43*
Domestic and personal service	296,480	0.47	2,424	0.42	12,820	0.52
Public service	*141,265*	*0.23*	*949*	*0.16*	*5,189*	*0.21*
Transportation	*480,095*	*0.79*	*4,480*	*0.77*	*27,002*	*1.11*
Manufacturing and mechanical industries	*2,011,722*	*3.22*	*32,875*	*5.64*	*216,996*	*8.90*
Agriculture, forestry, and animal husbandry	1,899,128	3.04	41,825	7.18	289,140	11.86
Extraction of minerals	*167,172*	*0.27*	*4,117*	*0.71*	*32,677*	*1.34*
Totals	6,461,551		100,946		650,244	

facturing and mechanical industries; 3.04 in Agriculture; and 0.27 in *Extraction of minerals*. But for every more fertile family, as here defined, in the *Professional service* class, there were 5.64 such families in the *Manufacturing* class; 7.18 in the Agriculture class; and 0.71 in the *Extraction of minerals* class. What these results mean is that families of more than average in the more-fertile families is not widely different from the proportion, always relative to the *Professional* group as 1.00, in which the several occupations are represented in the general male population, so far as concerns the first six occupations in Table 3. This means that in these six occupations the total fertility up to 1923, in the more fertile group with

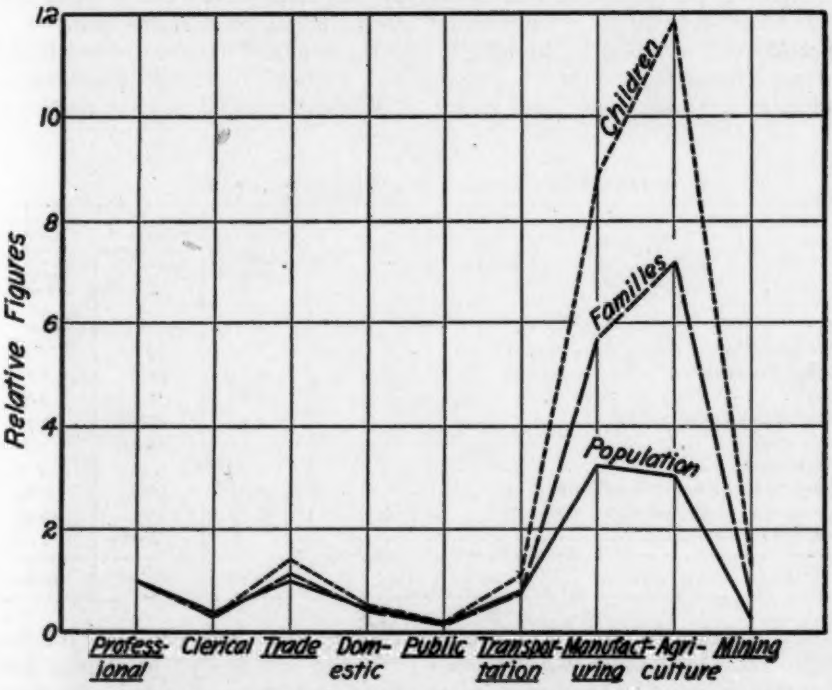

FIG. 2. RELATIVE POPULATION AND FERTILITY BY OCCUPATIONAL CLASSES
The solid line is the graph of column (b) of Table 3; the dash line of column (d); the dot line of column (f)

total fertility occurred in these three classes, in proportion to the male population of corresponding age, taking the *Professional* class as 1.00, from two to three times as often as they did in any of the six occupational classes discussed above.

3. The relative total number of children ever born, up to and including 1923, which we are dealing, was nearly in simple proportion to the size of the groups themselves, having regard to age, and when the *Professional service* group is taken as 1.00 in each instance. But in the three occupational classes *Manufacturing*, Agriculture, and *Mining* the case is quite different. Whereas there were 3.22 times as many males aged 45 and over in the

Manufacturing class in 1920 as in the *Professional* class, the females mated to males in the *Manufacturing* class had produced, up to and including 1923, 8.9 times as many children as had the females mated to the corresponding portion of the males in the *Professional* class, in the same period. In 1920 there were 3.04 times as many males 45 years of age and over in the Agriculture class as there were in the *Professional*. But the total production of children up to and including 1923, by the more fertile moieties in the classes, had been 11.86 times as great in the Agriculture class as it had been in the *Professional*. In the *Extraction of minerals* class there were only 0.27 as many males 45 years of age and over as there were in the *Professional* class. But the production of children up to 1923 had been 1.34 times as great in the former class as in the latter.

So far we have considered the populations, more-fertile families, and total children ever born, of the several occupational classes, only in relation to the *Professional* group taken as 1.00. This procedure gives a correct picture of the situation so far as strictly inter-class comparisons of the unit elements are concerned. But it does not permit entirely correct conclusions to be drawn in respect of the important question as to the proportionate contribution of each occupational group to the total population of the next generation. The proper base for the relative figures here is furnished by the *totals* of columns *a*, *c* and *e* of table 3, each taken as 100 per cent.

The results of treating the data in this way are shown in table 4 and fig. 3.

TABLE 4

Fertility of the occupational groups relative to the total population

OCCUPATIONAL CLASS (RECONSTITUTED)	PER CENT IN EACH CLASS IN 1920 OF MALES 45 AND OVER (a)	PER CENT OF MORE-FERTILE FAMILIES IN 1923 (b)	PER CENT OF TOTAL CHILDREN EVER BORN TO FAMILIES IN COLUMN (b) (c)
Professional service	*9.66*	*5.77*	*3.75*
Clerical occupations	3.33	1.66	1.10
Trade	*9.69*	*6.71*	*5.36*
Domestic and personal service	4.59	2.40	1.97
Public service	*2.19*	*0.94*	*0.80*
Transportation	*7.43*	*4.44*	*4.15*
Manufacturing and mechanical industries	*31.13*	*32.57*	*33.37*
Agriculture, forestry, and animal husbandry	29.39	41.43	44.47
Extraction of minerals	*2.59*	*4.08*	*5.03*
Totals	100.00	100.00	100.00

While the general trend of figure 3 is the same as that of figure 2, as it is in fact bound to be, figure 3 brings out an additional bit of information that is not shown by figure 2. What figure 3 shows is that in the first six occupational groups (*Professional*, Clerical, *Trade*, Domestic, *Public*, and *Transportation*) the more-fertile families in each group form a smaller percentage of the total number of more-fertile families than the males 45 years of age and over, in that same group, do of the total number of occupied males of the same ages. The single cross-hatched column is shorter, in every one

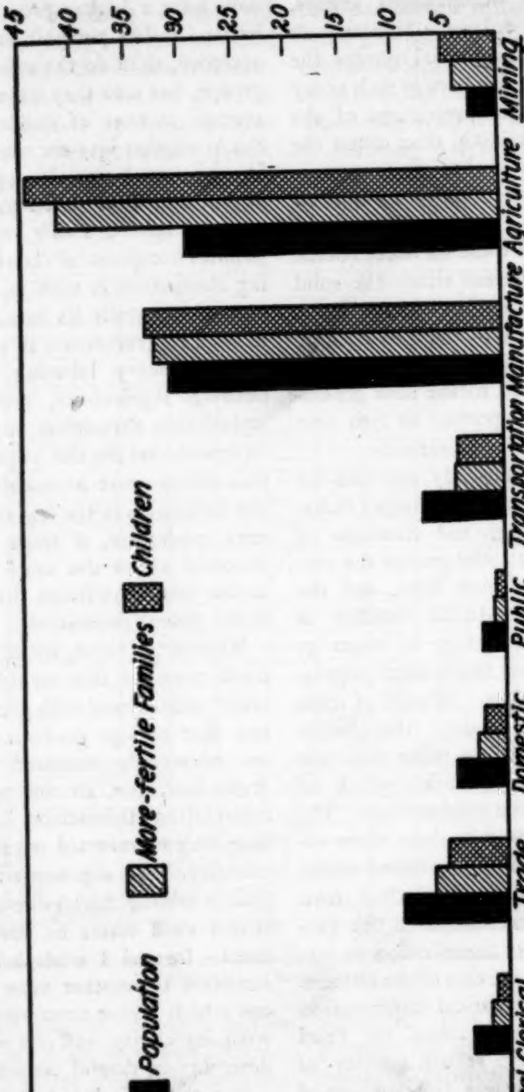

FIG. 3. GRAPH OF THE THREE PERCENTAGE COLUMNS OF TABLE 4

of these first six occupational groups, than is the solid column. Similarly in these same six occupational groups the number of children ever born in each group forms a still smaller percentage of the total number of children, than either the males 45 years and over or the more-fertile families in each group do of their respective totals. The double cross-hatched columns in these six occupational classes are shorter than either the solid or the single cross-hatched columns. These results mean that the men aged 45 and over in these six occupational classes have not contributed to the next generation in as high a proportion as their own representation in this generation.

The case is diametrically opposite for the last three occupational groups (*Manufacturing*, Agriculture, and *Extraction of minerals*). In these three groups the percentage of children ever born, and the percentage of more-fertile families is *higher* than the percentage of males 45 years of age and over in the total population of occupied males. In each of these three occupational groups the double cross-hatched column is taller than the single cross-hatched column, which in turn is taller than the solid column. The men aged 45 and over in these three occupational classes have contributed to the next generation more than their own proportionate representation in this generation. The excess contribution is particularly marked in the case of the farmers. It is convincing statistical confirmation of the conclusions reached by Pearl (1925) regarding the sexual activity of farmers, from an entirely different sort of data.

SOCIAL AND EUGENIC IMPLICATIONS

Summing the whole case up it appears that the great laboring groups, *Manufacturing*, Agriculture, and *Mining*, not only have a higher proportion of more-fertile families per unit of population so occupied, than do the other occupational groups, but also they have a much larger average number of children per family. Put in another way the case comes to this: In our population it appears that the *Professional*, Clerical, *Trade*, Domestic and personal service, *Public service*, and *Transportation* occupational classes are reproducing themselves in such manner as not to maintain in quite its present status their relative representation in the population. But the heavy laboring classes, *Manufacturing*, Agriculture, and *Mining*, are reproducing themselves in excess of their representation in the population. From this excess must necessarily be supplied the deficiences in the first six classes in the next generation, if these classes are to maintain about the same representation in the total population that they exhibit in the present generation.

What is the racial, social, and economic significance of this result? It has generally been viewed with great alarm. The fact that college graduates, from whom are necessarily recruited most of the *Professional* class, are not proportionately reproducing themselves has been more than once represented as a sort of national calamity. The arguments that this situation is wholly deplorable are so familiar that I shall waste no time in detailing them. Instead I wish briefly to direct attention to another view of the case—one which I have never seen stated before with any clarity, and one which I believe deserving of careful consideration.

In a theoretically ideal social organization there would obviously be an optimum number of persons engaged in each of the numerous differentiated occupations, which when integrated together are essential to the well-being and survival of the society as a whole. There is

theoretically an optimum number of teachers, lawyers, store-keepers, laborers, soldiers, and so on. But in actual human societies there is no extraneous, god-like determination of these optimum relative numbers in the occupational classes. Instead the actual existing number is determined by a process of natural selection, in which process economic factors are probably the most important element.

But another factor comes also into the case. The human units wear out faster in some occupations than in others, and therefore need to be replaced faster. Roughly speaking the occupational classes are listed in table 3 in descending order of average duration of life. The only important exception is in the case of farmers. And in that case, while the total duration of life of farmers is, on the average, somewhat greater than that of persons in occupations higher up the list, it is not so if attention is paid solely to *duration of economically productive life*. The old farmer is generally a retired farmer, so far as actual work at farming is concerned.

One other consideration also needs attention. This is not only an industrial country, but a country in which the increase of prosperity and well being is almost solely dependent now, has been for some time in the past, and presumably will be for some time in the future, upon the continued *growth* of industry. This is shown clearly in figures 4 and 5. Figure 4 is taken from Pearl (1922), and figure 5 from Rylands (1926).

What figure 4 demonstrates, I think, is

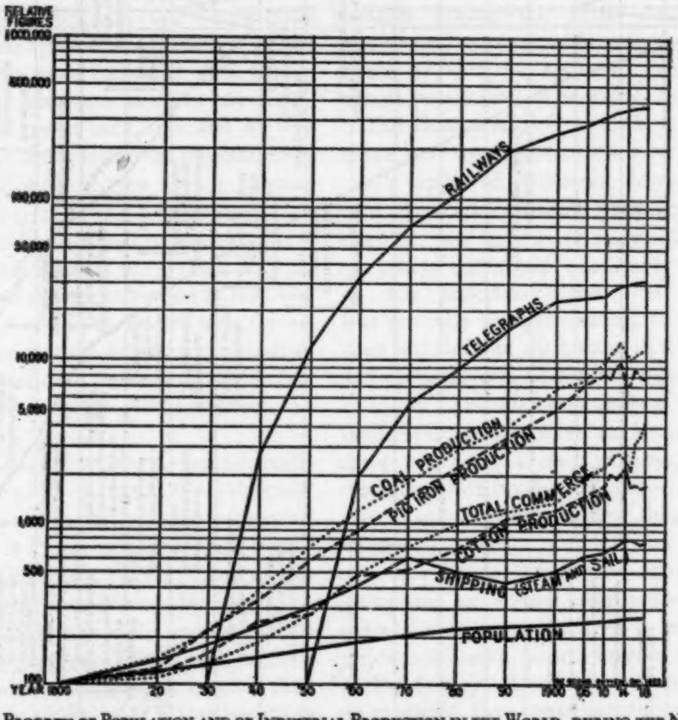

FIG. 4. THE PROGRESS OF POPULATION AND OF INDUSTRIAL PRODUCTION IN THE WORLD, DURING THE NINETEENTH CENTURY. (FROM PEARL, 1922)

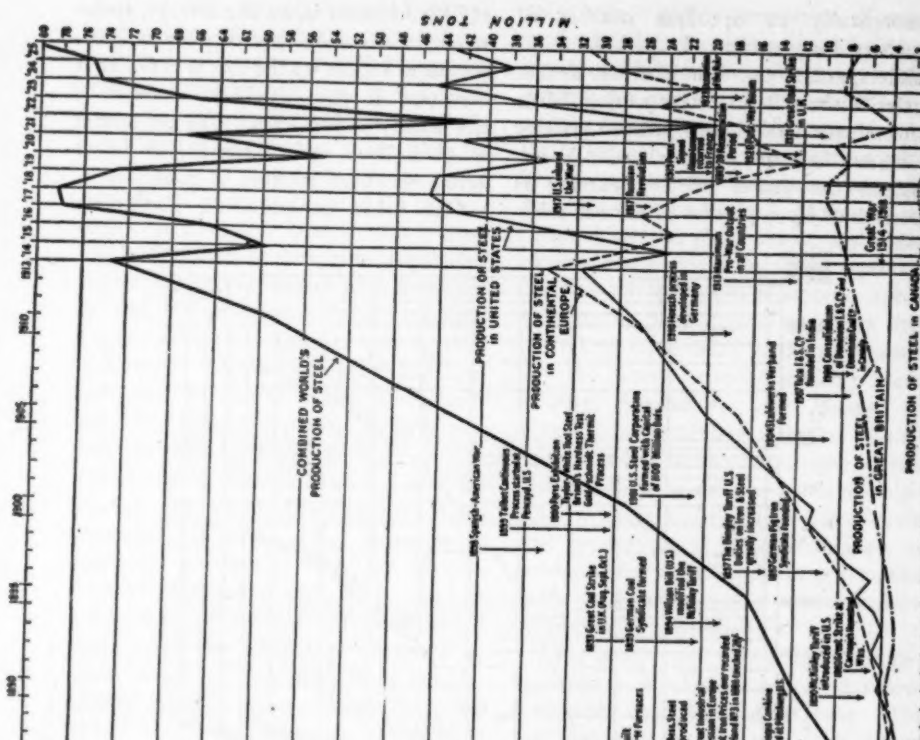

FIG. 5. THE WORLD PRODUCTION OF STEEL. (FROM RYLANDS, 1926. REPRODUCED, WITH THE AUTHOR'S PERMISSION, FROM PROOF COPY OF HIS

that in order to permit the population to increase roughly two and a half times, and enjoy the standards of living which prevail at the present time, it has been necessary to increase coal and pig iron production from 50 to 70 times, the cotton production 20 times, the railway mileage 3000 fold, and so on. It is only because the organization of industrial processes, inventions, and scientific discoveries have made possible the growth of industry of all sorts at the rates indicated that human beings have been able to enjoy the standard of living that they have and do, and at the same time permit the population to grow as it has. Figure 5 in a slightly different way tells the same story.

The hard facts shown in figures 4 and 5 mean further that all along there has had to be an increasing production of laborers, skilled and unskilled, in the manufacturing and mechanical industries. Machinery alone does not make a profitable factory. There must be workmen to run the machines.

While figure 4 relates to world conditions figure 5 shows that so far as the most important and basic of the mechanical industries is concerned, the same conditions prevail to a striking degree in the United States, considered by itself.

Now, I suggest that the findings of this paper regarding fertility in this country are not widely divergent from what they theoretically ought to be if our society is to continue in general prosperity and well-being, and continue to grow in these respects. In short we *need* to have laborers reproduce faster than the first six occupations on our list, in order first to take up the greater human wastage in the laboring classes, and second to permit of continued industrial growth and prosperity. Probably a sound economic structure of the country as a whole is in a very real and considerable sense dependent upon just this relationship. So far from being alarmed at the present situation, I am disposed to think that we should find serious cause for *real* alarm if it were markedly different from what it is. Though the biological processes involved are widely different in the two cases, the actual facts about differential human fertility are curiously reminiscent of what obtains among the social insects. A stable and economically sound society there, as with us, seems to demand an excess production of workers.

The facts set forth in table 4 plainly mean that some part of the next generation's supply of professors, doctors, lawyers, bankers, railroad presidents, and the like, will have to be recruited among the sons of the farmers and factory laborers of this generation. But what of it? Just precisely this relationship has always been true so far in the history of the world and probably will be true for a long time to come. And furthermore from just the same sources will have to be recruited some of the clerks, typists, small tradesmen, job-holders, brakemen, motormen, and various other less lofty citizens.

In the United States the agricultural group has for a long time produced far more than enough children to maintain its own industry, as has been shown by McFall (1925). These farm boys in excess, so to speak, have contributed in no small measure to the highest intellectual, social, and economic classes of our population. In fact the agricultural class has demonstrated an especial fitness to contribute sound stock to other occupational classes. I am disposed to believe that time will show that the industrial class in our large cities is, in already measurable and probably increasing degree, doing the same thing. Let one observe the origin of the most brilliant and able students today

in city high schools, both classical and technical.

Wheeler (1926) has ably argued, and made a sound case, that the next emergent "level" above mind is the social. He says (p. 435):

> One of the levels in which the situation, as it appears to me, is most open to investigation, is the social. Unfortunately the subject has been passed over by writers on levels with only a few vague remarks. Unfortunately, also, the science of comparative sociology has remained undeveloped. It has, in fact, fallen between two stools, because the sociologists have left the study of animal and plant societies to the biologists and the latter have been much less interested in these societies as such than in the structure or individual activities of their members. Apart from Forel and myself only a few investigators, like Espinas, Waxweiler, Petrucci and Deegener, have evinced a keen interest in nonhuman societies. Yet these, no less than human society, are as superorganisms obviously true emergents, in which whole organisms function as the interacting determining parts. Owing, moreover, to the loose and primitive character of the integration and the size of the components even in the densest societies, it is possible to ascertain the behavior of the parts and to experiment with them more extensively than with chemical and organismal wholes, since the parts of the latter are either microscopic or ultramicroscopic and are always so compactly integrated that analysis becomes very difficult and involves a considerable amount of statistical inference.

What may be said, with any critical insight, to be statistically known about differential human fertility indicates that in these phenomena we have an expression of a very subtle but far-reaching and extremely significant mechanism of self-regulation in the social super-organism. The falling birth rate and death rate and the type of occupational differential fertility discussed in this paper are primarily to be regarded, I believe, as adaptive regulatory responses—that is, biological responses—to evolutional alterations in the environment in which human society lives. In this environment the economic element is perhaps the most significant biologically. This is not the place nor the occasion for the elaboration of this theme. But one cannot but be impressed that the almost total neglect by eugenists of the obviously important influence of relatively simple economic factors upon the human situation with which they deal, and which they endeavor to account for in very far-fetched and highly inferential ways, is stupid.

Finally regarding the specific results set forth in this paper, I frankly do not see the usually alleged cause for eugenic alarm, for the reason that history demonstrates, I believe, that the superior people of the world have always been recruited from the masses, intellectually speaking, in far greater numbers than they have been reproduced by the classes. And in saying this I do not for one moment subscribe to the view that environmental influences have been the chief factor in the production of superiority. On the contrary I adhere firmly to Galton's view that heredity plays the principal rôle. But the almost infinite manifoldness of germplasmic combinations can be relied on, I think, to produce in the future, as it has in the past, Shakespeares, Lincolns, and Pasteurs, from socially and economically humble origins.

In order that there may be no misunderstanding it should be emphasized that what has been said in this paper relates entirely and solely to the *relative* or *differential* aspect of fertility, as between the several occupational classes, and *not* to the absolute fertility of the population as a whole or its component parts. That the population of the United States as a whole cannot go on increasing at its present rate per unit of time, and its component elements continue to enjoy the standards of living which they have in the past and do now, would seem to be obvi-

ous. This conclusion has been many times emphasized in recent years, by various students of the population problem, particularly East (1923), and the present writer (Pearl, 1922, 1924, 1925), both of whom have expressed, and still adhere to the view, that birth control is a rational and intelligent method of counteracting the evils of excessive population growth. There is nothing in the results or conclusions of the present paper which in the least conflicts with this prior conclusion. That the absolute levels of birth rate will continue to fall in all social and economic classes, as it has in the past, with increasing density of population, seems highly probable. All that is here argued is that a differential birth rate—a higher rate of reproduction in some social and economic classes than in others—is probably to be regarded as a biologically normal feature of the social and economic structure of large human groups, and that this fact is not necessarily a sound ground for eugenic alarm.

Finally to assume that this paper states that the unlimited reproduction of genetically unsound stocks is not a dysgenic menace, is simply a confession that the paper has not been read. It would, of course, be highly desirable if the reproduction of all stocks exhibiting traits universally admitted to be undesirable and known to be inherited, could be completely stopped. But it has yet to be demonstrated that either poverty or lack of membership in a social aristocracy are biologically inherited traits, though the inference is too often drawn that they are. The present paper is intended, in part, to show that the eugenic condemnation of whole social or economic classes, either directly or inferentially by the contention that only certain classes such as college graduates are eugenically desirable, is unwarranted by anything now known. While this is not the place to go into the matter in detail I am convinced that the current orthodox position of eugenics rests upon a fundamental genetic fallacy which largely invalidates some of its most important conclusions. This matter I hope to discuss in detail in the near future.

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NEW BIOLOGICAL BOOKS

The aim of this department is to give the reader brief indications of the character, the content, and the value of new books in the various fields of biology. In addition there will usually appear in each number one longer critical review of a book of particular significance. Authors and publishers of biological books should bear in mind that* THE QUARTERLY REVIEW OF BIOLOGY *can notice in this department only such books as come to the office of the editor. The absence of a book, therefore, from the following and subsequent lists only means that we have not received it. All material for notice in this department should be addressed to Dr. Raymond Pearl, Editor of* THE QUARTERLY REVIEW OF BIOLOGY, *1901 East Madison Street, Baltimore, Maryland, U. S. A.

THE TENDENCY TO SOCIAL LIFE

Being a review of *Les Sociétés d'Insectes, leur Origine–leur Évolution*, by William Morton Wheeler. Paris (Gaston Doin), 1926. $4\frac{1}{2} \times 7$; xii + 469. 18 Fr.

By Philip P. Calvert, University of Pennsylvania

This volume belongs to the series *Encyclopédie Scientifique*, one of which (by L. Cuénot on *l'Adaptation*) was reviewed at length by Prof. J. H. Gerould in the QUARTERLY REVIEW OF BIOLOGY for January, 1926 (pp. 119–123).

Perhaps the first impression which one receives upon seeing the title of this new book by Prof. Wheeler is that it is a French version of his *Social Life Among the Insects* (New York, Harcourt Brace & Co.) of 1923. The latter volume comprised the author's Lowell Institute lectures of March, 1922; the new book contains his discourses as exchange professor from Harvard University to the University of Paris in 1924–25. Prof. Wheeler takes pains to correct such an erroneous idea in his opening pages, telling us that while he has made use in part of the material of his *Social Life*, in which he emphasized the fundamental rôle of nutrition in the development of the various insect societies, he here proposes to treat, in a more technical way, of these four questions:

1. What are the social insects?
2. Can it be shown that they have had an evolution?
3. If so what are the characteristics of this evolution and what methods should be employed to elucidate them?
4. To what general causes or conditions can we refer this evolution?

The advance in knowledge of the habits of insects in the three years intervening between the appearance of Prof. Wheeler's two books is shown by the fact that his list of distinct cases of social organization in this Class has increased from 24 in 1923 to 30 in 1926. The additions are the Bethylidae, Masaridinae and Trypoxylonina among the Hymenoptera, the roaches (genus *Dasypoma*), the mole cricket (*Grylloptalpa*) and *Zorotypus*, a member of the recently discovered order Zoraptera. Twelve of the 30 groups listed in 1926 have definitely social members, the remaining 18 are believed to be in an imperfectly social (subsocial) condition. For these latter the existing data are too meager to make possible a satisfactory account of the development of

their social life. Here attention is given almost exclusively to the Aculeate Hymenoptera and the Termites. The rise and progress of social life in these groups are deduced from the fossils, now fairly numerous, morphological and taxonomic data and those of geographical distribution, together with comparisons of the habits of living insects.

The tendency to social life ("*tendance associative*" of Petrucci, 1906) is considered an appetition, like those of hunger and of sex, weaker but more continuous, less spasmodic and consequently less evident. Since all societies of insects are families, that is, affiliations between parents (usually a mother) and descendants, the attainment of the social condition is due to an increase in duration of her individual life and in her interest in her offspring. Pearl (1924) has suggested that the length of life of an animal is in inverse ratio to the activity of its metabolism. Prof. Wheeler thinks that the diminution of metabolic activity (which should, according to Pearl, prolong the life, especially of fertilized females) may be due to the fact that all the social and subsocial insects live in small cavities in soil or in wood, or in the interior of paper nests. Such abodes restrict or inhibit muscular movements. The living medium is dark, poor in oxygen, of uniform and rather low temperature. All these conditions tend to reduce metabolism and activity and to favor an accumulation of the fat in the body. The fecundity of the females is to a certain extent a function of their longevity as expressed clearly in the great size of the adult colonies of the higher termites, ants and the hive bee. On the other hand, the smallness of the completed colonies of various primitive ants and termites appears to be a consequence of the shorter life of the queen mother.

In his attempt to determine the phylogeny of the social Hymenoptera, Prof. Wheeler accepts the interpretation of Tillyard that certain recently discovered Permian fossils from Kansas represent a new order of insects, the Protohymenoptera, which by their wings (the only parts preserved) are intermediate between the Mecoptera (scorpion flies) and the Hymenoptera. The leaf-feeding sawflies of the families Pamphiliidae and Xyelidae (suborder Phytophaga) can be considered as the most ancient of living Hymenoptera. From such forms the entomophagous sawflies conduct us to the very archaic family of the Trigonalidae, referred by some to the Aculeate (stinging) Hymenoptera, by others to the Terebrantia (Parasitica); at the Trigonalidae these two series diverge from the ancient Phytophagous trunk. Near the base of the Aculeata the Bethylidae are to be placed and although this family is certainly very ancient and not to be regarded as ancestors of the social Hymenoptera, yet in the Scleroderma group of this family are realized conditions analogous to those in which the social habits of wasps, bees and ants originated. In this group the long-lived mother subsists on the same food as her young, is interested in them, licks them and can rear several broods successively. When the mother and her female descendants, or several females of different broods, are enclosed in the same receptacle with a larva of *Cyllene*, there is no rivalry between them, as one might expect, but on the contrary they coöperate to paralyze the prey and to lay their eggs on it in common.

Among the wasps, from *Synagris* to *Vespa*, the development of social life is characterized by the gradual appearance and differentiation of a caste of workers, by the increasing complication of the architecture of the nest, by the increase

in population of the colonies and by the larger size of the fertile female or queen. The annual development found in many members of this family fixes very definite limits to the extent of the population and retards or prevents all ulterior progress in social development.

The bees are the most numerous in species of all living Aculeates. They are imperfectly known and their taxonomy has yet to be worked out satisfactorily; different authorities have supposed them to be mono-, di-, or even tri-phyletic, although usually deriving them from the fossorial wasps (Sphecidae). In the development of their social habits, however, and in their nests they present an extraordinary parallelism to the Vespidae. The origin of wasp or bee communities from one or more than one female—monogyne or polygyne—is considered to be of minor importance depending on the mutual tolerance or animosity of the queens.

In seeking for the origin of ants, it appears to Prof. Wheeler that the group which merits the most serious attention is that of the Tiphiidae, and especially the genus *Elis* (*Myzine*). This family has affinities of structure and of habits with the Bethylidae, mentioned above. Six species of ants are known from the Eocene but they are not more primitive or more generalized than those of the amber and the latter are almost as highly specialized as those now living. These facts and the deeply rooted xerophilous tendencies of ants suggest their very probable origin in the Trias, if not at the end of the Permian, on great plains and interior continental plateaus, such as Australia presents today. Their first abode was on the surface of the soil, whence arose the subterranean, deserticolous and arboricolous habits, the last displayed by the most specialized genera of the whole family. Prof. Wheeler will not bring the ants across now submerged transatlantic or antarctic bridges from continent to continent and his inclination is toward a northern circumpolar centre of distribution for many of the genera.

The social bees although descended from the Sphecoids are, nevertheless, in many respects nearer to the social Vespoids than are the ants, descendants of (solitary) Vespoids. The explanation is no doubt to be sought in the evolution of the ants having been longer and more fertile in events.

Traits which the social Aculeates received from their solitary (non-social) ancestors comprise 1. A pronounced sexual dimorphism, 2. The storing of food for the young, 3. The construction of a nest, and 4. The defensive reactions of the female. As consequences of social life there have been added to these "solitary" bases a spermatheca which can preserve the sperm alive for so long a time that the fertilized female becomes potentially a hermaphrodite, capable of producing both sexes; a differentiation of the females into two castes, queens and workers, the latter again into workers properly so called and soldiers, while the male remains stationary and conservative; the mutual exchange of food between the members of the community (trophallaxis); the common utilization of collected stored food; the nest constructed by many instead of by one individual; and the defensive functions, more efficient and formidable than before, relegated to the workers or to the soldiers.

In the social aculeates the male has remained essentially in the condition of that sex as it existed in the solitary ancestors. He has not entered into the social activities; he is simply tolerated as indispensable for fertilization. The contrary is the case in the termites, where the various morphological specializations and the division of labor are shared equally by individuals of both sexes. From

the human point of view the termites thus appear as more perfectly social than the societies of aculeates and Prof. Wheeler asks whether, if, in some future metempsychosis, the choice were offered to one of us between the lot of an ant and that of a termite, the latter would be preferred!

Handlirsch (1903) placed the origin of the termites in the Cretaceous, but Prof. Wheeler thinks it may have been more remote. Fossil remains are not known from periods earlier than the Tertiary. Morphological data indicate their relationship to the roaches. As in the ants their present geographical distribution may be explained without recourse to intercontinental bridges.

The view here adopted as to the Mecopteroid origin of the Hymenoptera necessarily denies any genetic connection between the termites and the social aculeates. The fundamental differences between these two groups arise from the mode of formation of their respective colonies. In the former the colony is founded by a royal pair, in the latter by a fertilized female, either alone or accompanied by a swarm of workers. The termites, having preserved the ametabolic [the reviewer would prefer to say heterometabolic] type of ontogeny characteristic of the whole Orthopteroid series, have not realized the intimacy between the adults and the young which is correlated with the legless impotence of the immature aculeates. That the termites have not acquired the extraordinary instincts of the social aculeates is ascribed "sans doute" to their immediate ancestors not having traversed a stage of carnivorous and predatory habits and to their own life in great part in the midst of their food. The ultra-conservative habit of devouring wood and of living in the cavities thereof furnishes the key to comprehension of most of the social peculiarities of these insects. The cumbersome food and its slow digestion by the intestinal Protozoa have brought about the use of stomodaeal and proctodaeal foods with the resultant wide infection of the community with the flagellates and amoebae. Life in the interior of wood has led to degeneration or loss of the eyes, especially in the workers and soldiers, loss of pigment, often a thinning of the chitin, light-fleeing and water-seeking tendencies, and such means of defense as the cephalic glands of the soldiers and the building of solid nests.

While the descendants of an unfertilized hymenopterous female are generally males, there is no necessary connection between this fact and the polymorphism of the social insects. This is sufficiently proved by the termites in which both sexes arise from fertilized eggs and are equally polymorphic. In the Bethyloid Aculeates several genera have two forms of fertile females, one winged, the other wingless; here polymorphism precedes sterility. It is not improbable that the first ants may have preserved the dimorphism of the females after having become social. From such a beginning the reduction of the wingless females to workers may have occurred. This hypothesis may explain such observed conditions as the single apterous queen in the Doryline and other ants, the simultaneous presence of winged and wingless queens in the same colony (*Ponera*), or in different places (*Harpagoxenus*), the frequent existence of ergatomorphic queens (*Leptogenys*, *Onychomyrmex*), etc.

The polymorphism of the termites is not only more complicated in itself than that of the ants but it also affects both sexes equally. Soldiers are present in all termites, except in the genus *Anoplotermes* (where they disappeared second-

arily) while in the ants they are definitely developed in only a few genera. In termites the soldiers precede the workers phylogenetically. In ants the reverse is the case. In ants there is only one general type of soldier, the "mandibulate," which is also very general in termites, but is replaced in the higher members of this group by a second or "nasute" type. Ant soldiers differ less from the queen and workers of the same species, in the size and conformation of the head and mandibles, than is the case with termite soldiers and their respective workers and sexual forms.

The problem of polymorphism still preserves a "complexité exaspérante." At least six different interpretations of the origin of the castes can be formulated. Lack of data concerning the causes of blastogenic determinism render a discussion of some of these interpretations useless and attention is consequently directed here to the effects of different modes of feeding the larvae.

The slight differences between the workers and queens of social wasps and of bumble bees are susceptible of explanation by a quantitative difference in food. In the social bee *Trigona* the larger quantity of food supplied to the queen larva appears to hasten the development of ovaries, while the qualitative difference in the food of the two female castes of *Apis* appears to accelerate the maturing of the eggs in the queen and to reduce in her some parts which are better developed in the worker.

The great variety of nourishment supplied to the young of ants prevents the demonstration of a relation between food and the differentiation of the castes, but the first broods of single queens founding new colonies are always small workers. Later broods are workers of larger size and it is only after production of the largest workers that queens appear. This applies to other monogyne aculeates also and to termites. The soldier caste of ants corresponds rather to the workers of termites, phylogenetically if not functionally; it appears not to have been differentiated from that of the large workers before the middle of the Tertiary, to have arisen independently in most of the genera in which it is present and not to have acquired a definitive representation in the germ plasm.

If the views set forth in the early part of this book be accepted, Prof. Wheeler conceives that we might admit that the queens and workers of the Formicidae and the royal forms and soldiers in the Isoptera are really blastogenic, but that the other castes and especially the pleomorphic forms of workers and of soldiers are trophogenic. A very interesting discussion is given of considerations which bear on blastogenic versus trophogenic origins: 1. The extraordinary stability of the typical castes in the existing species of ants and of termites; 2. Their extraordinary constancy in the course of geological ages; 3. The difficulty of explaining the forms of gynandromorphic ants; and 4. The adaptive characters of soldiers and of workers. Space does not permit even a summary of this discussion here and its result is confessedly an *impasse*.

Thus far the first seven chapters. Of the activities which constitute the social medium of insects the trophic habits alone—owing to lack of time—are considered in Chapter VIII, but they dominate all the others. As "the fundamental nutritive *motifs*" are the leading feature in the book of 1923, its presentation here is less novel than other portions of the present volume. Less novel too are chapters IX and X, on the evolution of the associates and parasites, social and otherwise,

of social insects, which correspond fairly closely to Lecture V of *Social Life among the Insects*, and are indeed in some passages direct translations. In the final chapter (XI. Conclusions) a more extended comparison between insect and human societies is given than is contained in the first lecture of *Social Life*. The future of insect communities is considered in the light afforded by the history of the spread of two ants *Pheidole megalocephala* and *Iridomyrmex humilis* (Argentine Ant). Man will exterminate the terrestrial fauna and flora except that from which he can profit. Ants will long remain his rivals and his torment but they at last will fall before his indirect methods of attack, his modifying or suppressing the external conditions indispensable for their survival.

Les Sociétés d'Insectes, like all of Prof. Wheeler's work, is supplied with an extensive *Index Bibliographique*, here of 40 pages, under authors' names, arranged alphabetically, and then listed under topics, followed by alphabetical indexes of authors and subjects. There are, too, the usual passages at arms with Father Wasmann, which confirm the reviewer's opinion, formed years ago when following the controversial writings of T. H. Huxley and his antagonists, that it is a biological impossibility for two divergent minds to agree.

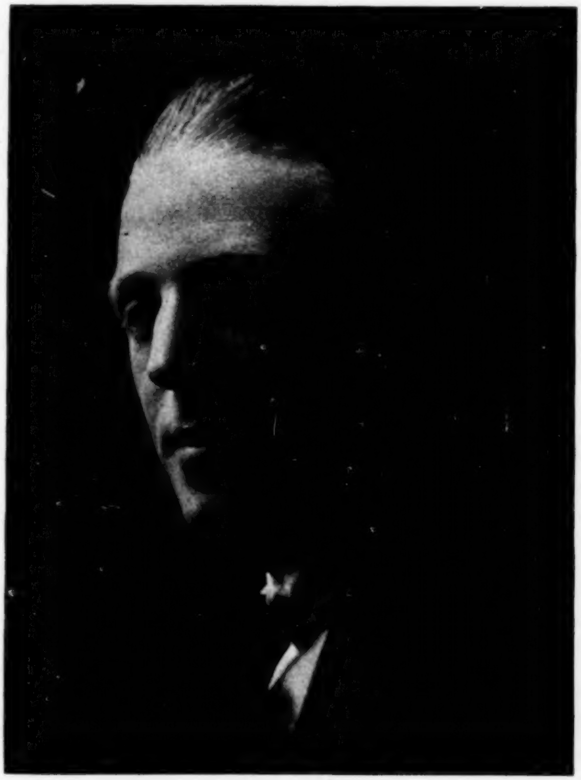
Prof. Wheeler has fully exemplified all the functions of a University—to preserve, to enlarge and to disseminate knowledge. He has not been content to pursue minute and tedious investigations in embryology, ecology, taxonomy and paleontology, nor with correlating these results with each other and with data drawn from other sciences. He has, on many occasions in books and journals, brought together the noteworthy generalizations of his fields of study, to the edification and—may we not say—delight of those who, like the reviewer, cultivate, with less skill, fewer and more distant acres. *Les Sociétés d'Insectes* is another case in point. Its publication in French will draw attention abroad, not too widely or generously given, to the achievements of American biologists, while it furnishes to all a more up-to-date résumé of the topics of which it treats than any other which we now possess.

BRIEF NOTICES

EVOLUTION

GENESIS *v.* EVOLUTION.
By Reginald Cock. *Elliot Stock*
2 shillings 5 x 7$\frac{3}{8}$; 77 London

The author of this little treatise is a practising physician in London. We take pleasure in presenting him as the second entrant into our *Fundamentalist Portrait Gallery*, reminding our readers that Rudolf Valentino has unfortunately passed away.



REGINALD COCK

Mr. Cock dedicates his book to the memory of "William J. Bryan, Esq." But it must not be inferred from this that Mr. Cock and Mr. Bryan are birds of entirely the same intellectual feathering. They are not quite, although both have equal faith in the infallibility of Holy Writ. Mr. Cock knows more about biology than the silver-tongued statesman ever knew about anything.

But all paradoxers reason queerly, as Augustus De Morgan long ago pointed out. And Mr. Cock is no exception. Thus he says:

> Now, it is to Homology and not to Analogy that scientists have been looking, since the evolution theory, in attempting the classification of animals,

and this is a very important matter to bear in mind. Structurally, the lowest animal (amoeba) is below the lowest plant (yeast cell) because the latter has a cell wall, whereas the former has not; yet the animal is without doubt higher functionally.

Common sense and Analogy teach us to group butterflies, birds, and bats together since they all have organs called wings; but Homology induces us to place in one class creatures outwardly so unlike as the rabbit and the whale. This has led to utter confusion and chaos.

Take, for instance, the third section of mammals, called *Monodelphia*, which comprehends all animals which give suck, from porpoises and whales to the monkeys and man. The variation of form presented by the Monodelphian mammals is so great as to defy even their leading characteristics being set forth.

They may be covered with hair or be hairless; they may have a hundred teeth or none at all; they may be gigantic monsters and inhabit the deepest seas.

A very interesting fact to point out here is that the placental method of reproduction is found in certain sharks, as well as in all true mammals. No trace of such a structure exists in any reptile or bird, and it is preposterous to think that the mammals have descended from the sharks. This highly complicated structure must have arisen quite independently in these two instances; and one is at a loss to understand how it could have developed by any process of slow, imperceptible variations, in accord with the evolution theory.

These similar structures, where genetic relationship is out of the question, tend to prove that Homology as a proof of genetic relationship is worthless.

There is Analogy in every Order; and Homology in all corresponding genera.

Every genus descends from a solitary progenitor or primitive couple—called into existence by the direct fiat of a designing Creator; this is why two of every kind, male and female, of every living thing of all flesh were taken into the Ark with Noah (Gen. vi, 19)—with the exception of fishes—in order to preserve the life of every genus. Linnaeus saw the world of organic life as composed of so many well-demarcated types, each separate, distinct, and immutable; each capable of producing its like *ad infinitum* and unable to vary except within very narrow and unimportant limits.

Instead of variability, we see invariability enduring for thousands of years.

What right, therefore, has anyone to assume a constant progress, when the observation of thousands of years, within the historic period of mankind, furnishes no proof of advance?

In the last chapter Mr. Cock answers categorically some of the "posers" (as he calls them) that Mr. Clarence Darrow put to Mr. Bryan at Dayton. Here he scintillates. Bishop Ussher is thrown overboard without a qualm; Cain married one of his sisters, which would now be sinful, but wasn't then; the Flood he approves of; Joshua did not really stop the sun, but did make it hesitate; Jonah was swallowed by *Carcharias vulgaris*.

The book ends with these words: "It is quite possible, and even probable, that the whole battle of Evolution will be fought over again in this country at no remote period, and the evolutionists will find it very much more difficult to substantiate their case once the community have become better informed."

We wonder.

THE EVOLUTION OF LIFE ON THE EARTH.

By Rev. James Morgan.

T. W. Childs and Sons
1 shilling *Teddington, England*
$4\frac{5}{8} \times 6\frac{7}{8}$; 6 (paper)

This naive little pamphlet, already in a second edition, settles the problem of evolution with a neatness and simplicity which can only command wondering admiration.

On the whole the principle of Evolution of Life on the Earth has been accepted as a natural process. There are, however, two views of this procedure. The one, that of progressiveness, by 'additions' of degrees of betterment; which was adopted by Darwin, and is generally held today. The other, that of the elimination of inferior characters, by what is termed 'Loss.' This means the casting off of the lower grades of life, by emergences from the main life-line.

Darwinism is incomplete. It has not a proper starting point: it assumes that all groups of life have their own special 'ancestors'; but it does not account for the *origins* of those ancestors. It stops before the end, the final purpose, is reached. Nor does it ac-

count for the 'variations' which form an essential element of its method. Take an example—The life-group to which Man and the ape are supposed to belong. It is held, today, that the 'ancestor' of this group is a small animal, *Tarsius*, of the monkey tribe. The origin of this ancestor is not accounted for. The same is affirmed respecting the ancestors of the other life-groups of the Tertiary Period. Nor is the final stage of Man's Evolution explained.

It will be seen that Man has been evolved through the vital principle of his own Main-life-line-strain—and *not* through any order of lower animal life.

The author does not fail to point out that Bateson, in his Melbourne address said: "In spite, therefore, of seeming perversity, we have to admit that there is no evolutionary change which in the present state of our knowledge we can positively declare to be, not due to 'loss.'"

We regret that lack of space prevents the reproduction of Mr. Morgan's entertaining, if not very illuminating, diagram, in which his theory is incorporated.

I BELIEVE IN GOD AND IN EVOLUTION.
By William W. Keen. *J. B. Lippincott Co.*
$1.25 $4\frac{3}{4} \times 7\frac{1}{4}$; 109 *Philadelphia*

In this fourth edition (eleventh thousand) of this sincere and appealing little tract of reconciliation, its venerable but sprightly author has added new material of three sorts; namely (a), some unimpeachable human tails; (b), an extensive array of evidence as to the similarity between man and animals in the structure of the internal ear; (c), a brief discussion of supernumerary mammae as ancestral vestiges.

THE EVOLUTION OF THE HORSE.
By Frederic B. Loomis. *Marshall Jones Co.*
$3.00 $5 \times 7\frac{1}{2}$; xvi + 233 *Boston*

A chapter in evolution, well told for the general reader, with excellent illustrations. "The story of the evolution of the horse as revealed by the study of the fossil remains is completed. It is fragmentary and even incomplete at some points, but in general we find a well defined succession of pictures which form a progressive series. The study of palaeontology proves the fact of evolutionary progress in the horse line, but leaves us in doubt about the causes behind it."

GENETICS

COLOUR BLINDNESS. (*Vol. II. Anomalies and Diseases of the Eye. Nettleship Memorial Volume. Part II. Eugenics Laboratory Memoirs XXIII. Francis Galton Laboratory for National Eugenics*).
By Julia Bell. *Cambridge University Press*
45 shillings $10 \times 12\frac{1}{4}$; 143; *London*
15 plates (paper)

The very high standard which the scientific world has learned to expect in the output of memoirs from Professor Pearson's laboratory is well maintained in this treatise on color blindness. The material is treated under three main heads: Color vision and its anomalies; total color blindness; congenital color blindness. The body of the text is followed by a name index to the chronological bibliography and to the authors of pedigrees, the bibliography which includes 425 titles, the descriptions of the pedigrees, and some 236 pedigrees. The subject is treated with exhaustive thoroughness. The volume will be a reference classic for all time. The chief conclusions regarding inheritance are:

The condition of congenital colour-blindness is strongly inherited and further it belongs to that group of inheritable diseases which is mainly manifested in males and transmitted by their unaffected daughters but not by themselves directly to their

sons. The condition however is not invariable in any single one of these characters and does not appear to conform at all rigidly to the laws of sex-limited hereditary defect of this type.

HANDBUCH DER BIOLOGISCHEN ARBEITSMETHODEN. Lfg. 182. Containing following articles: *Methoden der Züchtung von Reptilien und Amphibien*, by Paul Kammerer. *Allgemeines über Züchtung von Insekten*, by Franz Heikertinger. *Apterogenea*, by Hans Przibram. *Züchtung der Amphibiotica*, by Franz Heikertinger. *Züchtung von Orthopteren*, by Friedrich Zacher. *Züchtung der Corrodentia*, by Franz Heikertinger. *Züchtung von Rhynchoten*, by Franz Heikertinger.

Urban and Schwarzenberg

9.60 marks 7 x 10; 214 (paper) *Germany*

This number of the Abderhalden handbook will be of especial interest to geneticists because it gives detailed directions for the rearing under controlled cultural conditions of a wide variety of animals.

GENERAL BIOLOGY

A BIPOLAR THEORY OF LIVING PROCESSES.

By George W. Crile. *The Macmillan Co.*

\$5.00 $5\frac{3}{4}$ x $8\frac{3}{4}$; xv + 405 *New York*

Surgeons, or at least some surgeons, have traditionally always loved to philosophize, regardless of the consequences. Considering all the good they have done to suffering humanity in the practice of their proper art, it seems only reasonable that they should be permitted to speculate as much as they like, outside of the operating room and of office hours. Dr. Crile's book needs to be read by biologists with a certain kindly tolerance based upon some such general consideration as has been stated, because it contains an annoying amount of nonsense, along with a lot of interesting and valuable observations. Assuming the existence of such tolerance we recommend the reading of the book. The electrical phenomena associated with vital processes are an interesting and too much neglected aspect of biology, at least in strictly zoological and botanical treatises. The reader of Dr. Crile's book will learn a good deal about them. His thesis, however, that these phenomena are the essential causes of the activities of living things, rather than one of their effects, as pretty well everybody else believes, cannot be regarded as established by the painstaking collection of relevant and irrelevant evidence which he and his colleagues have brought together.

PRACTICAL MICROSCOPY. (*An Introduction to Microscopical Methods.*)

By F. Shillington Scales. *Alex. Eger*

\$2.00 5 x $7\frac{1}{2}$; ix + 332. *Chicago*

An American issue of the third edition of a useful elementary treatise on the use of the microscope. The author is University Lecturer in Medical Radiology and Electrology at Cambridge, England.

DER PARTIALTOD IN FUNKTIONELLER BETRACHTUNG. (*Ein Beitrag zur Lehre von den unspezifischen Reizwirkungen*).

By S. Gutherz. *Gustav Fischer*

3 marks 50 $6\frac{3}{4}$ x $9\frac{1}{2}$; v + 66 (paper) *Jena*

A very interesting, if sometimes speculative, discussion of the biological implications of the Arndt-Schulz law of the beneficial biological effects of minimal stimuli, taken in connection with Weigert's theory of partial death.

ÜBER DEN STOFFWECHSEL DER TUMOREN. (*Arbeiten aus dem Kaiser Wilhelm-Institut für Biologie, Berlin-Dahlem*)
By Otto Warburg et al. *Julius Springer*
16.50 Reichsmark *Berlin*
6 x 9; 263 (paper)

Dr. Warburg, in the *Kaiser Wilhelm Institut für Biologie* in Berlin, is doing some of the most interesting work now going on in the very lively field of cancer research, and it is a great convenience to have brought together in one volume this series of 21 recent papers by himself and his students. It ought also to be said that his researches on cellular metabolism are of quite as great general biological interest, as they are to the cancer specialist.

LIFE AND EVOLUTION. *An Introduction to General Biology.*
By S. J. Holmes. *Harcourt, Brace and Co.*
\$3.50 $5\frac{3}{4}$ x $8\frac{3}{4}$; v + 449 *New York*

The aim of this elementary textbook of general biology is "to present those aspects of biology which would best prepare the student for appreciating the great changes in our outlook upon the world which have resulted from discoveries and generalizations in regard to living forms." This is a commendable idea, and the book is entertainingly written to accomplish the purpose, as would be expected from the author's past performances. The book is extensively illustrated, and has a good index.

THE STREAM OF LIFE.
By Julian S. Huxley. *Watts and Company*
1s 5 x $7\frac{1}{4}$; 56 *London*

This little book constitutes number two of the Forum Series, distributed by the Rationalist Press Association. It consists of eight radio talks on various aspects of heredity, evolution and eugenics, delivered under the auspices of the British Broadcasting Company. The author apologizes in his preface for allowing them to be printed.

AN INTRODUCTION TO PRACTICAL BIOLOGY. *A Course of Work Based Chiefly upon the Plant and Arranged for Use Without Special Apparatus in Either the Classroom or the Home.*
By Norman Walker. *Isaac Pitman and Sons*
\$1.50 5 x $7\frac{1}{2}$; viii + 224 *New York*

A sound and interesting little elementary text book of general biology prepared for the use of adult students enrolled in the Tutorial Class movement in England. The drawings used as illustration are original and largely the work of the students in Adult Classes in Biology. A major part of the space is devoted to plants. The book merits the attention of teachers of evening, extension, and correspondence courses in this country.

L'ACQUARIO MANUTENZIONE FUNZIONAMENTO.
By Felice Supino. *Ulrico Hoepli*
18.50 lire $4\frac{3}{4}$ x $6\frac{1}{4}$; xvi + 201 *Milano*

An excellent, extensively illustrated, little manual of directions for the management of marine and fresh-water aquaria.

A NATURALIST'S PILGRIMAGE.
By Richard Kearton. *Cassell and Co., Ltd.*
7s 6d. 5 x 8; xii +245. *London*

This autobiography of the well-known wild life photographer and lecturer, makes entertaining reading. Kearton's

life has not lacked adventure, and one gets the impression that nothing very important has been lost in the telling. The book is illustrated with nine half-tone plates, some from the author's own superb photographs.

MALIGNANCY AND EVOLUTION. *A Biological Inquiry into the Nature and Causes of Cancer.*
By Morley Roberts.
Eveleigh Nash and Grayson
18 shillings 5½ x 8¾; 319 *London*

Every biologist should read this book. It contains a wealth of interesting material and valuable suggestions, whether one agrees with the author's views as to the origin of cancer, or does not. The fact that this significant contribution to biological thought is by a professional novelist is not without interest. It develops in novel ways Roux's old idea of the struggle of the parts in the organism.

THE SEASONAL DISTRIBUTION OF THE CRUSTACEA OF THE PLANKTON IN LOUGH DERG AND THE RIVER SHANNON.
By R. Southern and A. C. Gardiner.
The Stationery Office
2s 6d *Dublin*
6 x 9¾; 170 pp.; xv pls. (paper)

A detailed report upon a quantitative investigation of the plankton in Lough Derg and the mouth of the River Shannon, over a period of three years. While the chief attention is devoted in this report to the Crustacea, data on the phytoplankton, and some of the other elements of the zooplankton, are given.

HUMAN BIOLOGY

AMERICAN VILLAGERS. (*With an Appendix on the Social Composition of the Rural Population of the United States by Luther S. Cressman*).
By C. Luther Fry. *George H. Doran Co.*
$2.00 5¾ x 8½; 201 *New York*

This is an interesting contribution to a neglected aspect of human biology. It attempts to answer, on the basis of a sample of unpublished material in the archives of the Census Bureau, the following questions: "How many villagers are there? Are village populations declining? What kind of people live in villages? What do villagers do for a living? What are the distinguishing peculiarities of village populations? What functions do villagers perform?" The results bring out a number of interesting and unexpected points. About one-eighth of our population lives in villages. Villages are growing in population, not declining. Their population is more largely native white, and has a higher proportion of old persons than do city populations. Their gainfully employed inhabitants are more largely engaged in manufacturing pursuits than anything else, even in a purely agricultural region. Villagers have poor medical service. The statistical method used involves what amounts to a pretty heavy extrapolation, and one should be cautious about accepting detailed conclusions. There is no index.

HOW NATIVES THINK. (*Les Fonctions Mentales dans les Sociétés Inférieures*).
By Lucien Lévy-Bruhl. *Alfred A. Knopf*
$4.00 5¾ x 8½; 392 *New York*

It is a distinct service to have this anthropological classic available in English. The essential thesis of the book is

the formulation of what the author calls the "law of participation" to explain the workings of the minds of primitive peoples. Regarding their "law" Professor Lévy-Bruhl says (p. 76):

> At the moment it would be difficult to formulate this law in abstract terms. However, in default of a wholly satisfactory formula, we can make an attempt to approximate it. I should be inclined to say that in the collective representations of primitive mentality, objects, beings, phenomena can be, though in a way incomprehensible to us, both themselves and something other than themselves. In a fashion which is no less incomprehensible, they give forth and they receive mystic powers, virtues, qualities, influences, which make themselves felt outside, without ceasing to remain where they are. In other words, the opposition between the one and the many, the same and another, and so forth, does not impose upon this mentality the necessity of affirming one of the terms if the other be denied, or vice versa. This opposition is of but secondary interest. Sometimes it is perceived, and frequently, too, it is not.

The author devotes a great deal of space to bowling over Tylor's "animism" theory. But there are perhaps just as great, though different, weak spots in his own. However it is an important contribution to have emphasized and worked out the sociological factor in primitive thought with the shrewdness and skill that Professor Lévy-Bruhl has brought to bear on what must always remain an extremely complex and difficult problem.

DIE HYGIENE DER MENSCHLICHEN FORTPFLANZUNG. *Versuch einer praktischen Eugenik.*

By Alfred Grotjahn. Urban and Schwarzenberg
15 Marks 7 x 10; xi + 344 (paper) *Berlin*

This treatise by the professor of social hygiene at the University of Berlin, takes the sound position that if eugenics is ever to be practical it must concern itself with *groups*, that is populations, rather than with individuals. There is nothing that can be done to alter the hereditary constitution of an individual, whether it be good or bad, so far as anything now known in genetics demonstrates. But the hereditary constitution of a group or population, taken in a statistical sense, can obviously be altered, and this is done every day in laboratories of genetics with populations of lower organisms. Grotjahn devotes his book to a painstaking and thorough assembling of the data necessary for the formulation of a scientific program of group eugenics, or racial hygiene. It constitutes a useful reference work.

MEDICAL AND EUGENIC ASPECTS OF BIRTH CONTROL. *Vol. III.*
RELIGIOUS AND ETHICAL ASPECTS OF BIRTH CONTROL. *Vol. IV.*
Edited by Margaret Sanger.

American Birth Control League, Inc.
\$2.00 each. $5\frac{1}{4}$ x $8\frac{3}{8}$; 247 (paper), 240 (paper) *New York*

In the third volume of proceedings of the 1925 Birth Control Conference are papers by fourteen medical persons, and eight biologists. Mainly they have only ephemeral value. The most significant contributions appear to be those by Dr William Allen Pusey, and Dr. S. Adolphus Knopf.

The fourth volume contains twenty-eight papers, by as many different authors. Generally they deal with the vaguer humanistic aspects of the birth control movement. Three of the papers make significant contributions, these are "Conduct as a Science," by Professor Harry Elmer Barnes; "Problems of hedonistic sex relations," by Professor Adolf Meyer; and "The population problem in India," by Dr. Taraknath Das.

CONSERVATION OF THE FAMILY.

By Paul Popenoe. *Williams and Wilkins*
$3.00 5⅜ x 8; 258 *Baltimore*

This book is a piece of propaganda for a number of theses maintained by a small group of eugenists in this country. Scientifically its value, if it has any at all, is trifling. While operating in a different field of discourse its intellectual outlook and exegetical technique exactly parallel those of William Jennings Bryan and John Roach Straton in regard to religion and evolution, or of Irving Fisher and Howard A. Kelly in regard to prohibition.

LES RACES ET LES PEUPLES DE LA TERRE.

By J. Deniker. *Masson et Cie.*
$3.00 6¾ x 10; 745 (paper) *Paris*

The manuscript of the second edition of a classical anthropological text, first issued more than a quarter century ago, was practically ready for the printer when the author's lamented death occurred. By arrangement between the publishers and M. Deniker's family, parts of it have been edited and prepared for publication by various French specialists. It constitutes an excellent general text book of anthropology and ethnology.

RACE AND HISTORY. *An Ethnological Introduction to History.*

By Eugene Pittard. *Alfred A. Knopf, Inc.*
$6.50 6 x 9; xxiii + 505 *New York*

This volume in the History of Civilization series, written by the distinguished professor of anthropology at the University of Geneva, is intended as a companion and supplement to Febvre's *Geographical Introduction to History* in the same series. This develops the racial factor, in the sense of physical anthropology, whereas Febvre attempts to evaluate the environmental factor. Pittard's book is a solid, substantial contribution. It constitutes the best existing summary of the broad human meaning and significance of the wealth of detailed information which physical anthropology has accumulated. There is a bibliography of 300 titles and a detailed index.

DAS WACHSTUM DES KINDES.

By Eugen Schlesinger. *Julius Springer*
6 marks 7 x 10; 127 (paper) *Berlin*

A detailed and thorough critical review, with a bibliography of over 300 titles, of the literature on human growth, together with some original investigations by the author himself in this field. It is a reprint from Vol. 28, of the *Ergebnisse der inneren Medizin*. It will be a valuable reference work.

PREHISTORIC MAN AND THE CAMBRIDGE GRAVELS.

By Rev. Frederick Smith.
W. Heffer and Sons, Ltd.
7s.6d. 5½ x 8¾; viii + 121 *Cambridge*

This most entertaining book should be read by everyone interested in human pre-history, and who nowadays is not. For it is a wonderful record of enthusiasm and imagination brought to bear upon inherently unexciting material, chunks of flint from gravel pits. For more than 60 years the author has been collecting and studying what he believes to be the very earliest paleolithic worked flints, and trying by imagination and experiment to figure out how they were used and what for. It is greatly to be feared that his

conclusions will not be accepted in their entirety by the hard-boiled experts in prehistoric archeology. But his book is great fun, and he might be partly right. And his casualness is superb. Out of ten arrowheads on one plate he says that "three or four were culled from gravel in the Pepys Court of Magdalene College, two from paths in Trinity, and two from King's."

ALCOHOL AND LONGEVITY.
By Raymond Pearl. *Alfred A. Knopf, Inc.*
\$3.50 $5\frac{1}{2} \times 8$; xi + 273 *New York*

The author now publishes in book form the results of his investigations, extending over a number of years, of the effect of alcohol upon the duration of human life. The general result is that moderate drinkers show no impairment of longevity as compared with total abstainers. Heavy drinking materially shortens life. The experimental literature on the racial effect of alcohol is reviewed. This is a bibliography of 269 titles.

QUELQUES CONSEILS POUR VIVRE VIEUX.
By Maurice de Fleury. *A. Michel*
9 francs $4\frac{3}{4} \times 7\frac{1}{2}$; 304 (paper) *Paris*

A treatise on personal hygiene, containing much shrewd advice and a minimum of quackery. The author appears not to be a fanatic entirely opposed to all the pleasant things of life, as advisers about personal hygiene are too apt to be. On the contrary he preaches a doctrine of moderation, which general experience would indicate to be sound.

ZOOLOGY

BIRDS IN ENGLAND. *An Account of the State of Our Bird-Life and a Criticism of Bird Protection.*
By E. M. Nicholson. *Chapman and Hall*
12 s. 6 d. $5\frac{1}{2} \times 8\frac{3}{4}$; xix + 324 *London*

This extraordinarily interesting and original book deals systematically with the ecological relation between birds and men in the British Isles at the present time. The discussion hinges about bird protection. The author demonstrates with great wealth of detail what idiotic mistakes zealous but ignorant uplifters can make. Two long chapters on the balance of the bird population, with an analysis of the reasons for the alterations in the proportionate numbers of different species, constitute a first rate contribution to evolution theory. There is an excellent index, and a list of the scientific names of all birds mentioned in the text. Finally must be mentioned the eight beautiful woodcuts by E. Fitch Daglish with which the book is illustrated. They have high artistic value.

LES MOLLUSQUES D'EAU DOUCE. (*Encyclopédie Pratique du Naturaliste XXIV*).
By E. Chemin (Preface by L. Joubin).
Paul Lechevalier
25 francs $4\frac{1}{2} \times 8$; 185, 15 plates *Paris*

An excellent little handbook which introduces the reader to the fresh-water molluscs in the happiest possible way. It takes up successively all of the genera found in France. Under each genus the most common species is first discussed in considerable detail, as to its structure, its physiology, its mode of life, habits, etc. Then the other species of the genus are described with sufficient detail so that

they can be easily identified with the help of the illustration. The whole is very well done, and results in a book which has real charm, and will inevitably attract young people who chance to read it to observe and perhaps really study fresh-water molluscs. Why do we not do this sort of thing in this country? The whole effort of biological teaching here seems to be to make the subject as forbidding and unattractive as possible, by talking about nothing but physics, chemistry and mathematics, and by confining the student strictly to a dingy laboratory.

MARVELS OF REPTILE LIFE.
By W. S. Berridge.
Thornton Butterworth, Ltd.
6 s 5¾ x 9; 256 *London*

For the "marvellous" purposes of this book and the series to which it belongs, amphibians are counted as reptiles. The author excuses this on the ground that the book "does not purport to be a scientific treatise." It is in fact a pleasantly written popular bit of natural history, well illustrated by half-tone plates of photographs, most of which seem to be original and to have been made in a zoological garden. The author makes some very up-stage remarks about the palatability of the diamond-back terrapin, which the editorial staff of The Quarterly Review of Biology, as loyal denizens of the Maryland Free State, cannot allow to pass unchallenged.

PERSONALITY OF WATER-ANIMALS.
By Royal Dixon and Brayton Eddy.
Brentano's
$2.50 6 x 8¼; xxv + 254 *New York*

An abundantly and well illustrated hodge-podge of cheap natural history writing about animals that live in water. The book has no unity or coherence, and the depth of its philosophy is sufficiently indicated by the following quotation:

> Perhaps some day we shall learn that Fishes are but undeveloped birds, that the Garden of Eden was a submarine garden and Adam and Eve had scales and fins. Then, perhaps, we shall look upon our lesser brethren more sympathetically. The greatest of all teachers—Christ—knew the value of marine education for he chose as his disciples men thoroughly acquainted with the sea.

BIOLOGIE DER TIERE DEUTSCHLANDS. (*Lieferungen* 7–14).
Edited by Paul Schulze *Gebrüder Borntraeger*
5½ x 8⅜ (paper) *Berlin*

Lief. 7, 1.80 Marks, 100 pp.
Hymenoptera I. By H. Bischoff.
Amphibia. By A. Remane.
Lief. 8, 1.80 Marks, 94 pp.
Hymenoptera II. By H. Bischoff.
Lief. 9, 1.65 Marks, 69 pp.
Ephemoptera. By Georg Ulmer.
Reptilia. By A. Remane.
Lief. 10, 1.80 Marks, 70 pp.
Plecoptera. By Ed. Schoenemund.
Coleoptera I. By H. v. Lengerken.
Lief. 11, 1.65 Marks, 64 pp.
Nematodes. By Gerhard Wülker.
Lief. 12, 1.95 Marks, 68 pp.
Coleoptera II. By H. v. Lengerken.
Lief. 13, 3.60 Marks, 113 pp.
Trichoptera. By Georg Ulmer.
Lief. 14, 2.55 Marks, 68 pp.
Euphyllopoda. By H. Spandl.
Bryozoa. By Ernst Marcus.

The high standard set in the earlier numbers of this collected work, already noticed in The Quarterly Review of Biology, is well maintained in the numbers here listed. When completed the whole will make a valuable reference work.

A NATURALIST'S NOTE-BOOK IN CHINA.
By Arthur De Carle Sowerby.
North-China Daily News and Herald
Mex. $8.00 $6\frac{1}{8} \times 9\frac{3}{4}$; 270 *Shanghai*

With the exception of a few early chapters this popular treatise on the natural history of China deals exclusively with animals lower in the scale than mammals or birds. The book is eminently readable, and contains a good many interesting original observations. It makes no attempt at scientific profundity, but is just a pleasant general survey of the lower animal life of China. The book is quite extensively illustrated with photographs and line drawings, the latter mostly by the author himself. There is no index.

I MOLLUSCHIE E LE CONCHIGLIE.
By Carlo Piersanti. *Ulrico Hoepli*
48 lire. $4\frac{1}{8} \times 6\frac{1}{4}$; xiv + 527 *Milano*

This manual first discusses in a series of introductory chapters the general biology, anatomy, physiology and ecology, of molluscs and then follows with a systematic portion for the identification of the Italian species. The work is well done, and will surely prove a useful aid to beginning Italian zoologists. There is an extensive bibliography, a good index, and 403 illustrations. It is unfortunate that each separate half-tone cut is outlined by an ugly black border.

THE HISTORY OF PROTOZOOLOGY.
By F. J. Cole. *University of London Press*
3 shillings $5\frac{1}{2} \times 8\frac{3}{4}$; 64 *London*

This book is made up of two charming lectures on the history of our knowledge of Protozoa, delivered at the University of London. The author stirs the reader's curiosity and desires by saying "these lectures are based on material for a general history of Zoological Discovery which I have been collecting for many years." This general history of zoology will be eagerly awaited, now that so tempting a sample has been furnished. There is a bibliography of some seven pages.

THE ANT. (*A Popular Account of the Natural History of Ants in all Countries.*)
By Edward Step. *Hutchinson and Co.*
7s. 6 d. 6 x 9; xii + 276 *London*

A compilation, to some extent from first-hand sources, of information about the biology of ants, for popular consumption. The book is abundantly illustrated with half tone plates. There are no specific bibliographical citations. The author seems to have but a meager first-hand acquaintance with American literature on the subject. There is an index.

BRITISH SPIDERS. *Their Haunts and Habits.*
By Theodore H. Savory.
Oxford University Press
$2.00 $4\frac{3}{4} \times 7\frac{1}{4}$; xii + 180 *New York*

The first six chapters of this well written little handbook deal with the general biology of spiders, their anatomy, and the principles of their taxonomic characters. The remainder of the book is devoted to descriptions, with fairly well worked out keys for identification, of the species most commonly found in Great Britain. The book is sufficiently illustrated, mostly with original line drawings, and is well indexed. One chapter is devoted to directions for keeping spiders in captivity.

DIE GIFTPRODUKTION BEI DEN TIEREN VON ZOOLOGISCH-PHYSIOLOGISCHEN STANDPUNKT. (*Zugleich ein Hinweis auf funktionelle Beziehungen zwischen Giften, Hormonen, Gerüchen*).

By J. Strohl. *Georg Thieme*
2 marks 6¾ x 10; 56 (paper) *Leipzig*

A reprint in separate form of a series of papers by the Swiss zoologist Strohl which amount to a *Sammelreferat* of what is known about the production of poisons by animals, unified by the point of view that poisons are mainly by-products of the normal physiologic-metabolic economy, and may have important functional relations and uses besides being poisonous to other animals.

TIERISCHES LEUCHTEN UND SYMBIOSE. (*Vortrag gehalten in der Zoologisk-Geologiska Foreningen zu Lund am 5. October 1925.*)

By Paul Buchner. *Julius Springer*
2 marks 70 5¾ x 8½; 58 (paper) *Berlin*

This lecture assembles and discusses evidence in support of the thesis that light-producing animals cultivate, in their special phosphorescent organs, luminous bacteria, which are passed on from generation to generation "like a holy flame." There is a brief bibliography of literature relating to symbiosis and bioluminescence.

A PRACTICAL HANDBOOK ON RAT DESTRUCTION.

By C. Leopold Claremont. *John Hart*
3s. 6d. 4¾ x 7½; 180 *London*

The chief reliance of this treatise is upon poisoning. Extensive directions are given for its practical employment. The book is an outcome of the Rats and Mice (Destruction) Act, which was passed by Parliament in 1919, and marks at any rate the beginning of a systematic attempt of the English to get the upper hand of these pests.

IL NATURALISTA VIAGGIATORE

By Gestro E. Vinciguerra. *Ulrico Hoepli*
14 lire. 4½x 6; xv + 204 *Milano*

A little handbook for the field naturalist which gives directions for collecting, labelling, and preserving specimens. There is unfortunately no index. A translation of this book, with some editing for American conditions, would be a useful aid to our students.

DAS PROBLEM DER ZELLTEILUNG PHYSIOLOGISCH BETRACHTET.

By Alexander Gurwitsch. *Julius Springer*
16.50 marks 5½ x 8; vii + 218 (paper) *Berlin*

This volume serves the useful purpose of bringing together in summarized and unified form the results of the author's investigations, extending over many years, on the physiology of cell division. Some enterprising American publisher should arrange for an English translation of this book.

THE CATTLE GRUBS OR OX WARBLERS, THEIR BIOLOGIES AND SUGGESTIONS FOR CONTROL. (*U. S. Department of Agriculture Bulletin No. 1369*).

By F. C. Bishopp, E. W. Laake, H. M. Brundrett, R. W. Wells.
Government Printing Office
25 cents *Washington, D. C.*
6 x 9; 119 (paper)

A thorough and detailed account of the biology of the two economically important species of *Hypoderma*. There is a

bibliography of 112 titles. This bulletin is the record of a fine piece of research in natural history.

BOTANY

STUDIES IN ADVANCING STERILITY. *Nos. 1 and 2. Part I. The Amherstieae. Part II. The Cassieae.*
By John McLean Thompson.
University of Liverpool Press
4 s. 6 d. each *Liverpool*
$8\frac{3}{4}$ x 12; No. 1, 54 (paper)
No. 2, 47 (paper)

The general purpose of the first of these extensively and beautifully illustrated morphological memoirs from the Hartley Botanical Laboratories of the University of Liverpool is

> to illustrate from the floral development of members of the *Amherstieae*, a tribe of Caesalpinoid *Leguminosae*, the importance of a knowledge of ontogeny in any systematic discussion, and the light which it may throw on the problems of a group as a whole. From the evidence adduced it is held that the chief problem with which the *Amherstieae* are faced in the ontogeny of their flowers is an advancing sterility of their androecium. The entire tribe is held to be evolving towards total sterility, by perversion to petaloidy, or by complete inhibition, of the primordia of the stamens.

There is a bibliography of eighty-eight titles.

The second memoir proceeds along similar lines to the first. In the *Cassieae*

> that sterilisation of the gynoecium has occurred and still occurs is accepted on the evidence for *Cassia* itself, though the single carpel which is typical of the tribe seems remarkably stable. On the other hand it has been shown that while complete sterilisation of the gynoecium is typical of one genus, with separation of the sexes, it is occasional in another without any apparent biological advantage being attained. The tribe as a whole is therefore held to be evolving towards total sterility, by perversion, arrest and inhibition of the primordia of its essential floral organs.

There is a bibliography of fifty-seven titles.

BAKTERIEN-CYCLOGENIE. (*Prolegomena zu Untersuchungen über Bau, geschlechtliche und ungeschlechtliche Fortpflanzung, und Entwicklung der Bakterien.*)
By Günther Enderlein. *Walter de Gruyter*
20 marks $6\frac{3}{4}$ x 10; viii + 390 (paper) *Berlin*

In this book the distinguished entomologist of the Zoological Museum of the University of Berlin enters upon a new and widely different field, the life cycle of bacteria. He states that the book was written in substantially its present form in 1915–16, apparently with the idea of delicately but firmly establishing priority over Löhnis, who published his first important paper in this field in 1916. The book starts with a brief historical review of the literature on the morphology of bacteria. This is followed by descriptive sections on the comparative cytology and general morphology of bacteria, based upon the author's own work, and illustrated by scale drawings. Then follows a chapter on the reproduction asexual and *sexual* of bacteria. This leads to a long section on the life cycle of bacteria. The remainder of the book deals with such questions as classifications, infectious diseases, etc., in the light of the author's discoveries and conclusions. Finally there is (a) an index of the new findings, (b) a bibliography, (c) a complete chronological list of all of the author's own publications, 285 in number, and (d) a general index. A new and somewhat bewildering terminology is invented and used throughout. But the talk is of new facts, if they are facts, so new words are excusable.

HANDBUCH DER BIOLOGISCHEN ARBEITSMETHODEN. Lfg. 186. Containing the following articles. *Die Bestimmung der Titrationsacidität in Pflanzenextrakten und ähnlichen gefärbten Flüssigkeiten. Die Bestimmung des formoltitrierbaren Stickstoffes in Pflanzenextrakten und ähnlichen gefärbten Flüssigkeiten. Die Bestimmung präexistierender Substanzgruppen (Säure, formoltitrierbarer Stickstoff, Kohlehydrate usw.) in Pflanzen*, by Heinrich Leurs. *Nachweis der Assimilation des Luftstickstoffes*, by Alfred Koch. *Methoden zur Bestimmung der Aufnahme organischer Stoffe durch die höhere Pflanze*, by Walter Kotte. *Methoden zur Bestimmung der Assimilation der Kohlensäure aus der Luft und aus dem Wasser*, by Heinrich Schroeder.

Urban and Schwarzenberg

4.80 marks 7 x 10; 102 (paper) *Germany*

Details of technique in the study of plant metabolism, particularly on the biochemical side.

THE STUDY OF VEGETATION.
By E. Pickworth Farrow.

Blackie and Son, Ltd.

2 s. 4⅞ x 7¼; 23 (paper) *Glasgow*

This pamphlet is a reprint of an article in *Discovery* which had for its purpose to arouse popular interest in the study of ecology. It is well done.

LIFE OF PLANTS.
By Sir Frederick Keeble.

Oxford University Press, American Branch

$1.75 5 x 7½; xii + 256 *New York*

The distinguished professor of botany at Oxford, adds, by this volume, to his already distinguished reputation as a writer of popular biology. In brief space, and with great clarity and real literary distinction, it gives an account of the essentials of plant morphology and physiology, including genetics. The book is well illustrated and indexed and we recommend it highly to the general reader, as well as to the teacher and beginning student.

THE PHYSIOLOGY OF PLANTS. *The Principles of Food Production.*
By George J. Peirce. *Henry Holt and Co.*

$3.00 5½ x 8½; x + 363 *New York*

A treatise on plant physiology which follows novel lines, at least in the general philosophical viewpoint from which the well-known subject matter is approached, and according to which it is arranged. We strongly commend the book. It is readable. It is scientifically sound. It is no dreary, dull compilation, as at least nine-tenths of all the biological text books which go over this editorial desk are. It has *Geist*.

A LABORATORY GUIDE FOR GENERAL BOTANY.
By C. Stuart Gager.

P. Blakiston's Son and Co.

$1.25 5¼ x 7¾; x + 203 *Philadelphia*

The third edition of a well-known and thoroughly established set of laboratory directions for a course in general botany.

COURS DE BOTANIQUE, *à l'usage des établissements de l'Enseignement moyen.*
By O. Terfve and P. Turlot.

Ad. Wesmael-Charlier

50 cents 5¾ x 8¾; 341 *Namur*

This book is a masterpiece of tedium, containing no fact discovered since 1875 and no theory proposed since 1850. The

plant kingdom is described as if it were embalmed. Each chapter is headed by the portrait of a Belgian botanist; throughout the text no others are mentioned; but the poor Belgian child who is taught from this frightful work will not be led to follow in their footsteps. Doubtless a translation would suit the purposes of the Tennessee Board of Education.

ÉTUDES FLORISTIQUES SUR LA RÉGION DU LAC SAINT-JEAN. *Contributions du Laboratoire de Botanique de l'Université de Montréal, No. 4.*
By Frère Marie-Victorin.
Université de Montréal
$1.00 6 x 9; 174 *Montreal*

A local floral list.

EINE BOTANISCHE TROPENREISE. (*Indo-Malaiische Vegetationsbilder und Reiseskizzen*).
By G. Haberlandt. *Wilhelm Engelmann*
9.50 marks 6¾ x 9; x + 296 *Leipzig*

This is the third edition of a classical treatise on tropical vegetation, first issued in 1893. The text is little changed from its original form, though, as the author points out, the conditions of travel and of botanical work in Java have greatly changed in thirty-five years. The book remains a delight, however.

CATALOGUE OF THE PRINTED BOOKS ON AGRICULTURE PUBLISHED BETWEEN 1471 AND 1840 WITH NOTES ON THE AUTHORS.
By Mary S. Aslin.
Rothamsted Experimental Station Library
10 shillings 6 x 9¾; 331 (paper) *Harpenden*

A fine piece of bibliographical work, which will stand as a solid contribution to the history of agriculture. The book will be found useful for reference by historians of botany and, to a lesser extent, zoology.

MORPHOLOGY

LOGIK DER MORPHOLOGIE IM RAHMEN EINER LOGIK DER GESAMTEN BIOLOGIE.
By Adolf Meyer. *Julius Springer*
18 Reichsmark *Berlin*
6¾ x 10; vi + 290 (paper)

There is no getting around the fact that this is a dull book. We have struggled with it on several occasions, and emerged each time more depressed than before. It is not that there is anything wrong with it. Every statement seems unimpeachable. But 279 pages of precise discussion of the logical implications of the working definitions and procedures of biology is not only a lot, but also is steadily, ineluctably, and devastatingly *boring*. For anybody, if there is such a person, who likes this sort of thing, this is a good book. But our guess is that it will not make much difference in the conduct of any biologist's life.

THE COMPARATIVE ANATOMY, HISTOLOGY, AND DEVELOPMENT OF THE PITUITARY BODY.
By. G. R. de Beer. *Oliver and Boyd*
12s. 6d. 5½ x 8¾; xix + 108 *Edinburgh*

This volume in the series of *Biological Monographs and Manuals* edited by Crew and Cutler, is a careful piece of straight morphological research on the pituitary

body. Following an introductory chapter on technique the structure and development of the pituitary is followed through the great animal groups from mammals to cyclostomes. The book is illustrated by eleven plates (some colored) and one hundred and eighteen drawings in the text. There is a bibliography covering four pages and an index. It will be a useful reference book.

OUTLINES OF COMPARATIVE ANATOMY OF VERTEBRATES.
By J. S. Kingsley. P. Blakiston's Son and Co.
$4.00 6 x 9; x + 470 *Philadelphia*

The third edition, considerably revised, of Kingsley's standard textbook. The bibliography has been brought down to date. It is an excellent text and its past success should be continued in this new edition.

MORPHODYNAMIK. *Ein Einblick in die Gesetze der organischen Gestaltung an Hand von experimentellen Ergebnissen. Abhandlungen zur theoretischen Biologie, Heft 23.*
By Paul Weiss. Gebrüder Borntraeger
2,70 marks 6½ x 10; 43 (paper) *Berlin*

A philosophical—and in some degree metaphysical—discussion of the problems and data of experimental morphology. This address will particularly interest those who are struggling with the emergent evolution doctrine.

HISTOIRE DE L'ANATOMIE COMPARATIVE.
By J. Chaine. E. Daguerre
24 fr. 5½ x 8; vi + 461 (paper) *Bordeaux*

This stout volume forms the historical portion of a large work on comparative anatomy, of which one previous volume has appeared, and two more are announced. The author, who is a professor of the Faculty of Sciences, at Bordeaux, proceeds in a pleasant leisurely way, with much philosophical discussion, written in a beautifully clear style. The book is a welcome addition to the meager literature on the history of zoology. It is well indexed.

PHYSIOLOGY

BIOLOGICAL RELATIONS OF OPTICALLY ISOMERIC SUBSTANCES.
By Arthur R. Cushny.
The Williams and Wilkins Co.
$2.00 5½ x 8½; ix + 80 *Baltimore*

This third series of lectures of the Charles E. Dohme Memorial Foundation at the Johns Hopkins Medical School constitutes a welcome addition to a neglected field of pharmacology, and, more broadly, of general biology. The untimely death of Professor Cushny, so soon after these lectures were delivered, has left a real gap in the scientific world. His sound, deep scholarship and ripe wisdom were never more clearly shown than in these lectures. Their broad biological significance is indicated by the following concluding remarks:

> I have dwelt at what may have appeared to you prodigious length upon the properties of optical isomers in living tissues, because it seems to me that here we have a clearer connection between the behaviour of substances in the test tube and in the living tissues than is often met with. For I think it is beyond question that the differences in the reaction of the two components of atropine on the salivary glands on the one hand and to such substances as camphor-sulphonic acids on the other are of the same essential nature, each depending on the union of two optically active substances. We have seen that they are conditioned in part by the asymmetry, in part by some specific configuration including the presence of

HO; of these, asymmetric carbon is present in every organ and cell, but the configuration necessary for the development of its results is limited to very few organs. The reaction is so definite when it is present that it may be taken as a test for the presence of this configuration in the tissues.

TIERPHYSIOLOGISCHE ÜBUNGEN.
By Paul Krüger. *Gebrüder Borntraeger*
30 marks *Berlin*
7 x 10½; xxv + 518 (paper)

This is a combined text and laboratory guide for a comprehensive course in general physiology. If the work called for is done with any thoroughness at all, there would be required at least a year's course of three laboratory periods a week. The author states that he has never been able to get it all into one semester. The course starts with some physical chemistry, followed by some physiological chemistry. Then the vital phenomena themselves are tackled, *Reizphysiologie, Stoffwechselphysiologie*, etc. There is nothing novel in this plan, nor in the book. It is simply a well developed course along lines which have been standard and conventional in the teaching of general physiology in this country for some twenty years past.

THE FURTHER STUDIES ON DECREMENTLESS CONDUCTION.
By Genichi Kato. *Nankōdō*
6 x 9; 163 *Tokyo, Japan*

This is a detailed report of a series of investigations by the author, who is professor of physiology at Keio University, and his students, in further elaboration and support of his conclusions that:

1. The *intensity* of nervous impulse does not suffer decrement during passage along the narcotised region of nerve. 2. The *rate* of the nervous conduction suffers no decrement during the passage along the narcotised region. 3. The nervous impulse of *subnormal intensity* (for instance the nervous impulse evoked in the relatively refractory period) suffers no decrement during conduction along the narcotised region of nerve. 4. The nervous impulses of *varying intensities* are extinguished at the *same* stage of narcosis, that is the intensity of nervous impulse has no influence at all on its ability to travel through the narcotised region of nerve. 5. The *all or none principle* is valid in the narcotised region of nerve. It must be noted that the quantity of 'all' (the size of maximal response) becomes gradually less as the narcosis deepens, but at any stage of narcosis the size of nervous impulse is not dependent on the strength of stimulus applied, it gives always the maximal response possible in that stage of narcosis or none at all. 6. The nerve loses by narcotisation its excitability and conductivity at the *same* time.

Thus, according to the new theory of decrementless conduction, the nerve suffers no *qualitative* but only quantitative change by narcotisation, whereas the old theory of decrement maintains that not only narcosis but also any other abnormal condition of nerve bring about qualitative change (decrement and inapplicability of all or none law).

MORE LIGHT. *A Simple Account of How the Brain Works.*
By Sidney Cameron.
Williams and Norgate, Ltd.
3s. 6d. 5 x 7½; xiii + 75 *London*

This is an original and interesting speculation. Its conclusions, with most of which probably no biologist will agree, are as follows:

The brain is an organ for generating and distributing nerve energy. The energy is derived from the blood, and stored in a chemically unstable form in the grey cells of the cerebral hemispheres, medulla, and spinal cord. The distribution to the muscles and organs is effected through the nerve filaments. All nerves are efferent, that is, the flow of energy is in one direction from the centre to the periphery. The optic, the auditory, the dental, the tactual nerves offer no exceptions to this rule. In all cases the nerves convey outgoing currents, which impart muscular or sensory tonus to the sense organs or

muscles. The body, which includes the brain and nervous system is primarily a neuro-muscular organism. Perceptions and memories are as extraneous to it as the reflected light which illumines the inert body of the moon. Memory is not to be explained by the morphology of the brain cells, but is a phenomenon that is deducible from the nature of space-time. By assuming appropriate attitudes, and by suitable adjustments of the muscular system, particularly those parts of it which are concerned in the production of speech, the body is able to pick up signals from the past, and thus reconstruct it in idea with the aid of mental and verbal imagery.

THE SECRETION OF THE URINE.
By Arthur R. Cushny.

Longmans, Green and Co.
$5.50 $5\frac{3}{4}$ x $8\frac{3}{4}$; xii + 288   *New York*

This second edition of Professor Cushny's well known treatise in the series of *Monographs on Physiology*, appeared only after his death, but fortunately he had read the galley proofs, so that as Professor Starling says in a note, it puts "on record his considered views on a subject in which his theory serves at the present time as the starting-point for all the work that is proceeding in different laboratories." Much new material has been reviewed in this edition. Over 200 titles have been added to the bibliography, which now totals to 593 references. The book is well indexed and will long serve as a standard reference source.

TRAITEMENT DES MALADIES MENTALES PAR LES CHOCS.
By C. Pascal and Jean Davesne.

Masson et Cie.
60 cents $5\frac{1}{4}$ x $7\frac{1}{2}$; xv + 182 (paper)   *Paris*

Stimulated probably by the recent successes in treating general paresis with malaria, the authors have brought together in this little book much of the literature on the use of the many substances which have from time to time been injected into the veins of the sick with the hope of startling them into recovery. Unfortunately, no attempt has been made to evaluate the methods described, to sum up what has been accomplished, or to give the experience of the writers, so one is left with the impression of having read little more than a plan on paper.

LA SÉCRÉTION INTERNE DU PANCRÉAS ET L'INSULINE.
By André Choay.   *Masson et Cie.*
$2.00 $6\frac{1}{4}$ x $9\frac{1}{2}$; xx + 570 (paper)   Paris

A thorough-going review of the physiology of the pancreas, documented with a bibliography of 1377 titles. The book is divided into four parts: Historical résumé of the period before the discovery of an internal secretion of the pancreas; experimental diabetes and the demonstration of the existence of an internal secretion; pancreatic extracts now employed therapeutically under the name insulin; physiology of the internal secretion of the pancreas. A supplementary chapter deals with the reciprocal relations between the pancreas and other endocrine glands. The book is well indexed.

CARBOHYDRATE METABOLISM AND INSULIN.
By John J. R. Macleod.

Longmans, Green and Co.
$6.00 $5\frac{3}{4}$ x $8\frac{3}{4}$; xii + 357   *New York*

The purpose of this monograph is stated by its distinguished author, the co-discoverer of insulin, to be "to give a

comprehensive review of the advances which have been made in our knowledge of the metabolism of the carbohydrates during recent years, and more especially since insulin became available. This is preceded by an account of the researches which led up to the isolation of this hormone and a review of the evidence that it is derived from the Isles of Langerhans of the pancreas. The nature of the diabetic condition which supervenes upon withdrawal of insulin from the body is also discussed." It is needless to state that the treatment is thorough and exhaustive. Extensive bibliographies follow each of the twenty-one chapters. There is a detailed index.

STUDIES IN INTRACRANIAL PHYSIOLOGY AND SURGERY. *The Third Circulation. The Hypophysis. The Gliomas. (The Cameron Prize Lectures, delivered at the University of Edinburgh October 19, 20, 22, 1925).*
By Harvey Cushing. Oxford University Press
$3.25 *American Branch, New York*
6⅛ x 9¼; xii + 146 (paper)

The first of these delightful and epoch-marking lectures deals with the cerebrospinal fluid and the spaces through which it circulates. The second treats of the pituitary body and its disorders, while the third discusses brain tumors in general and the gliomas in particular. The lectures are followed by bibliographies of 70, 49, and 62 titles respectively, these lists being limited to the papers of the author, his students, and their students. The whole forms a record of consistent first-rate research achievement, of which all concerned may well be proud. The volume is sparsely but significantly illustrated, and well indexed.

BIOCHEMISTRY

BIOCHEMIE DES MENSCHEN UND DER TIERE SEIT 1914. *Wissenschaftliche Forschungsberichte. Band XII.*
Edited by Felix Haurowitz.
Theodor Steinkopff
7 marks 6 x 8¾; xii + 148 (paper) *Dresden*

A condensed conspectus of the progress of biochemistry—on the animal side—since 1914, which gives individual references to more than eleven hundred bibliographical titles. It makes a very useful reference work.

CERTAIN ASPECTS OF BIOCHEMISTRY.
By J. C. Drummond, A. V. Hill, H. H. Dale, and L. J. Henderson.
University of London Press
12s. 6d. 5½ x 8¾; viii + 313 *London*

This volume prints thirteen lectures given in the University of London in the summer session of 1925, by four distinguished physiologists and biochemists. The lecturers and subjects treated are as follows: Dr. H. H. Dale, The Chemical Control of Certain Bodily Functions: I, The Control of the Circulation in the Capillary Blood-vessels; II, Active Principles of the Pituitary Body; III and IV, The Pancreas and Insulin. Prof. J. C. Drummond: I and II, Modern Views on the Mechanisms of Biological Oxidations; III, Certain Aspects of the Rôle of Phosphates in the Cell; IV, The Vitamins. Prof. L. J. Henderson: Blood and Circulation from the Standpoint of Physical Chemistry: I, The Physico-chemical Changes in Blood during the Respiratory Cycle; II, The Synthetic Description of Blood as a Physico-chemical System; III, Deductions concerning the Circulation. Prof. A. V. Hill: I, The Physical Environ-

ment of the Living Cell; II, Lactic Acid as the Keystone of Muscular Activity.

The book as a whole is a notable performance. It serves as a very readable, and at the same time authoritative, bird's-eye view of recent progress in nearly all of the more lively fields of physiology. All of the authors maintain a high level of excellence in their treatment of their respective subjects, but Prof. L. J. Henderson's section deserves especial mention as a masterpiece of bold and successful scientific generalization, popularly expounded with consummate skill.

SEX

GESCHLECHTSLEBEN UND FORTPFLANZUNG DER ESKIMO. (*Abhandlungen aus dem Gebiete der Sexualforschung, Band IV, Heft 6*).
By Hans Fehlinger.
A. Marcus und E. Weber's Verlag
RM 2 $6\frac{3}{4} \times 10\frac{1}{4}$; 36 (paper) *Bonn*

A useful compilation from the literature of what has been recorded regarding various aspects of the biology of reproduction and of sex among the Eskimos. The material is discussed under six heads, as follows: General remarks about the Eskimo; marriage; morality; pregnancy, parturition and rearing of the child; fertility; race-crossing. There is a bibliography of 23 titles. The observations upon which the treatise is based are, in the nature of the case, mainly rather casual and scattered. Putting them together as Fehlinger has done shows where the great gaps in our knowledge are, regarding this basically important branch of human biology in such an anthropologically significant group of people as the Eskimos.

MODERN MARRIAGE.
By Paul Popenoe. *The Macmillan Co.*
\$2.50 $5 \times 7\frac{1}{2}$; xiii + 259 *New York*

Detailed directions as to how to get a wife and how to keep her. Nothing whatever is left to either imagination or instinct. The chapter on courtship, entitled "How?" is wonderful.

FORTSCHRITTE DER SEXUALWISSENSCHAFT UND PSYCHANALYSE. *Band II.*
Compiled by Dr. Wilhelm Stekel; Edited by Dr. Anton Missriegler and Emil Gutheil.
Franz Deuticke
18 marks *Leipzig*
$6\frac{3}{4} \times 9\frac{1}{4}$; iv + 575 (paper)

This is a voluminous and depressing record of bad dreams and sad case histories. The volume includes thirty-three papers, and a few book reviews. The only amusing one we have been able to find in the lot is a learned disquisition upon Martin Luther's scatological tendencies, and even here there is a strenuous, though unsuccessful, attempt to preserve the prevailing psychoanalytic gloom. Probably all these papers, with their abundant technical terminology, are good science, and therefore to be approved of, but it is difficult to refrain from inquiring "good for what?"

KÖRPER UND KEIMZELLEN. *Teilen I und II.*
By J. W. Harms. *Julius Springer*
33 marks (each) *Berlin*
$5\frac{3}{4} \times 8$; x + 516 und 508 (paper)

A thorough, detailed, well illustrated review of the extensive literature on the relation between the gonads, secondary sexual characters, and the general structural and functional economy of the body.

It is a welcome and useful addition to the literature of general biology. The author is professor at Tübingen. There is a bibliography covering forty-eight closely printed pages, and an index.

BIOMETRY

MEASUREMENTS OF THE CUBICAL CONTENTS OF FOREST CROPS. *Being a Critical Investigation into the Methods of Measuring Sample Plots with Special Reference to the Liability to Error. Oxford Forestry Memoirs No. 4.*
By M. D. Chaturvedi.
Oxford University Press
$3.50 *American Branch, New York*
$7\frac{1}{2} \times 10\frac{3}{4}$; xv + 142 (paper)

This detailed mathematical discussion of the measurement of the volume of an individual tree, and of the total volume of wood in a forest stand, is chiefly of interest to professional foresters. All of the different methods which have been suggested are critically reviewed. None appears to have more than somewhat unprecise relative accuracy. There is a bibliography covering about four and a half pages.

SUR LES SEMI-INVARIANTS ET MOMENTS EMPLOYÉS DANS L'ÉTUDE DES DISTRIBUTIONS STATISTIQUES. *Skrifter utgitt av Det Norske Videnskaps-Akademi i Oslo. II. Hist.-Filos. Klasse 1926, No. 3.*
By Ragnar Frisch. *Jacob Dybwad*
$7 \times 10\frac{3}{4}$; 87 (paper) *Oslo*

Treats of the relations between the semi-invariants, moments, and factorial moments of frequency distributions, and of the use of generalized Bernoulli numbers in dealing with these parameters. The binomial and hypergeometric distributions are considered in detail.

PSYCHOLOGY AND BEHAVIOR

THE MEANING OF PSYCHOLOGY.
By C. K. Ogden. *Harper and Brothers*
$3.00 $5\frac{1}{2} \times 8\frac{1}{4}$; xxi + 326 *New York*

This is a popular *résumé*, in the simplest language possible, of the present state of knowledge and opinion in the field of psychology. The author's purpose is primarily exposition rather than conversion to any particular doctrine. With shrewd critical insight he steers a happy course among the warring isles of the psychologic archipelago, and gives the voyager a fine view of the pleasant scenery on each, without subjecting him to any dangers or hardships at all. The popularity of the book is well deserved. It has an excellent index.

INTELLIGENCE AND IMMIGRATION.
By Clifford Kirkpatrick.
Williams and Wilkins
$4.00 6×9; xiii + 127 *Baltimore*

This volume, which constitutes the second number in a series of *Mental Measurement* monographs, first summarizes the results of other investigators in so-called intelligence testing of different race stocks in this country, and reaches the conclusion that these studies have shown that "in general the representatives of the newer immigration, especially the Latins, have less intelligence than the Americans or those of the older immigrant stock." There then follows a detailed account of the author's own investigation of a group of Massachusetts school children falling into the following groups: French Canadians, Finns, Italians, and Americans.

The tests used were the "Illinois Examination," and the Army Beta. The following conclusions were reached:

> Americans are but slightly, if at all superior to the Finns in intelligence. Both are far above the Italians, and the French Canadians, taken as a whole, rank between these two extremes. These differences are accentuated by a linguistic handicap. The demonstration of a linguistic handicap means that these important differences in intelligence are less than they appear, but it fails to disprove their existence.

There is a bibliography of 146 titles and an index.

BRAINS OF RATS AND MEN.
By C. Judson Herrick
University of Chicago Press
$3.00 5¼ x 7¼; xiii + 382 *Chicago*

This book is a serious attempt to develop a consistent view of human psychology and personality upon a groundwork of what is known of the morphology of the vertebrate nervous system. In this latter field the author is an acknowledged master. Therefore his views, on the philosophical, and to some extent metaphysical questions which this attempt implies and involves, are entitled to a respectful hearing. They are extremely interesting, if perhaps not always fully convincing. There is a bibliography of thirteen pages, and an index.

TELLING ON THE TROUT.
By Edward R. Hewitt.
Charles Scribner's Sons
$2.50 5¾ x 8¼; xi + 166 *New York*

An enthusiastic fisherman contributes a good deal more than the expected expert advice about flies, rods, and other tackle. Mr. Hewitt has made many original observations on the habits and behavior of different species of trout in various parts of the world. Also he has carried out some interesting observations and experiments on the vision of fish. The book is a worthy addition to the ecological and behavioristic library. It unfortunately lacks an index.

IS NATURE CRUEL? *A Partial Answer to the Question. Experiences of Big Game Hunters and Others While Under the Attack of Wild Beasts.*
By J. Crowther Hirst. *G. Bell and Sons*
1 shilling 4⅛ x 6⅝; 61 (paper) *London*

This little book defends the odd thesis that the killing of living things for food by predatory animals, particularly the large carnivora, is neither a particularly painful nor fearsome process for the killed. The evidence adduced is the testimony of various persons who have been mauled by lions, tigers, and bears, or have witnessed such maulings, to the effect that they did not feel much pain at the time. It is a curious book, now in a second edition.

DE OMNIBUS REBUS ET QUIBUSDEM ALIIS

THE MILLENNIUM AND MEDICAL SCIENCE.
By David Nicholas Schaffer, M.D.
Wilbur Needham
$2.00 5½ x 8; 371 *Evanston, Ill.*

On pages 356, 357, and 358 of this "Wonder Book of the Age" is one single sentence containing 509 words, by actual and time-consuming count. We believe this is by no means the longest sentence in the book. We only counted this one because we got lost in it, both subject and predicate escaping our clutches together. This unfortunate stylistic char-

acteristic of a book warmly recommended by publishers and author to

(a) Those who have read "Black Oxen," and
(b) Those who have not read "Black Oxen,"

makes it a little difficult to follow the plot though there are many nice, sonorous words, fairly printed on a medium quality of paper. Chapter XIX is entitled "The Theory." We have carefully read it through six times. But regretfully we are obliged to say that we cannot find out what the theory is. To our dull perception there seems to be nothing in the chapter but an involved and verbose recital of some of the elementary facts of the physiology of human reproduction, with a lot of mostly erroneous drivel, about hormones, enzymes, vitamines, glands, and bacteria. The book has some diagrams, but all attempts to capture the big idea by Mark Twain's formula of "treeing it in the pictures" have failed. The one bit of real entertainment derived from this welter of stupid dullness is to be found in a diagram lying between pages 140 and 141, which carefully distinguishes between the "Arterial Blood Stream" and the "*Venus* Blood Stream" *in the pelvic region*. Thus proving that "God's in his heaven," etc.

A DICTIONARY OF MODERN ENGLISH USAGE.

By H. W. Fowler. Oxford University Press
$3.00 5 x 7½; viii + 742 *New York*

This book is a joy. While dictionaries are not popularly supposed to make good reading, this is an exception. It is replete with sly humor and entertaining quips. At the same time it is the most thorough and authoritative treatise which exists in compact form on the difficulties and niceties of the English tongue. Everyone who does any writing, and particularly every scientific man, should have this enormously useful book constantly at his elbow.

INTRODUCING REGINALD

The increasing complexity of our editorial life has made it necessary for us to employ an office boy. His name is Reginald. He is young, but exhibits the shrewdness usual in the lower anthropoids. We have considerable hope that he may be trained to do the necessary simple tasks of the office.

But he has already shown a disturbing, though characteristic, mischievousness. As the last page proofs of this number were going to the printer Reginald slipped in the following contribution, which he says he made up with scissors and paste from things he found lying about on the editorial desk.

Debate About Evolution

PRO

Coming now to the evidence afforded by systematic zoology as to the course of evolution, we see at once that inferences from it involve a rather dangerous assumption. This assumption is that some species stood still and retained the ancestral form and habits whilst allied species became modified. Nevertheless there are many cases in which this assumption appears to be sound. Squirrels, whose form and habits are familiar to all, are very much alike wherever they occur all over the world; the Canadian squirrel is especially familiar to Londoners as it has been introduced into the Royal Parks and is rapidly multiplying. It can often be seen leaping from branch to branch in Kensington Gardens. But in Canada there exists another and rarer variety, the so-called flying squirrel, which has a parachute-like expansion of skin reaching from the knee to the elbow. This squirrel is capable of taking colossal leaps of seventy to eighty yards in length during which it "volplanes" through the air supported by its parachute. Does anyone doubt that this species has been developed from the normal type by becoming continually adapted to making longer leaps? Thus systematic zoology can show what course evolution

has followed in the case of an isolated species amongst the other species of a genus, when the majority have a uniform type of structure and habits, and the same reasoning applies to an isolated genus amongst the normal genera of a family.

The reasoning becomes much more doubtful when we ascend higher in the scale, because it becomes more difficult to be sure that one family or one order has remained unmodified and can be taken as representing ancestral structures whilst others have changed.

The case of the flying squirrel, however, raises another question which is of far-reaching significance. This squirrel lives to-day in the very same woods as those inhabited by the common squirrel: yet the latter appears to thrive quite as successfully as the flying squirrel. The peculiarities of the flying squirrel must therefore have arisen in a different region, where trees were sparse and where it was exceedingly dangerous to descend to the ground, but having evolved its peculiar habits there it has spread into more normal situations.

(By Professor Ernest W. MacBride, F.R.S. in "*Evolution in the Light of Modern Knowledge*," pp. 250–252, 1925.)

CON

I noticed recently that a cow, while grazing, used her tail vigorously to drive away the flies. I began to think as to how I should account for the existence of cows' tails, if I were an evolutionist. In the early stages of the development of cattle, of course they would be tailless. When their bowels moved there was left at the opening a small deposit of fecal matter. This attracted the flies. In order to get rid of the flies the animal twitched the flesh at this part of the body. This was continued for many generations till it resulted in a protuberance as a permanent feature of cattle. Continued stretching of this protuberance to drive the flies from other parts of the body caused it to lengthen, and after a few millions of years the tail became a universal character of the species. Additional vertebræ were added to the dorsal column, and the caudal appendage developed into its present proportions.

But in my evolutionary thinking I struck a snag: If the cow's tail was developed by use, why should it have stopped at its present dimension? The cow stretches her tail in vain toward her shoulders and her head. The flies are especially busy about her eyes, but she cannot brush them off with her tail. According to the evolutionist, we may assume any length of time we may think necessary; but with all the billions of years at our disposal, the shortness of the cow's tail, as long as it is, proves that evolution is an error.

Again I noticed that the tail of the horse, though the two animals subsist on similar food and grew up in similar environment, is very different from the tail of the cow. The vertebræ in the cow's tail are nearly uniform in size from end to end, while those of the horse are smaller and smaller toward the outer end. Moreover the cow has a bunch of long hair, somewhat like a paint brush, at the end of her tail, while the horse's tail has long hair from end to end.

I have wondered too at the supposed development of the rattles on the tail of the rattle-snake. According to the evolutionists there must have been a time when the snake had no rattles. If he attempted to rattle without success, is it likely that he would continue to try to rattle for a sufficient number of generations to have made the rattles come? The snake's tail is even more difficult to account for under the theory of evolution, than the cow's.

(By W. R. Coppedge in the Charlotte, North Carolina, *Observer*.)

Reginald has been reprimanded.

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